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JOURNAL OF ANATOMY

NERVE ENDINGS IN THE MUSCLES OF THE FROG

By DR N. KULCHITSKY

Anatomical Department, University College, University of London

The nerve endings in the muscles of the frog were discovered by Kühne (1861). This was the first advance made in the investigation of nerve endings in muscles after the discovery of the direct connection between nerve and muscle fibres (Doyère, 1840). From this time on, numerous investigations were carried out, which point to the interest taken by histologists in this question. It is necessary to remember, however, that Kühne's discovery was made at a time when no very precise histological methods were established and the microscope itself had hardly reached the brighter days of its development. The investigators of that time could at best use the water-immersion system, constructed for the first time by Hartnack in 1859. This is why, together with valuable discoveries which have retained their importance up to the present time, we find in histological literature a great number of observations, made by very prominent investigators, which now have only a historical importance. I venture to pass over these observations without discussion. Indeed, the period when the investigations of authors undoubtedly began to acquire a definite character, dates back to the end of the seventies or the beginning of the eighties of the last century, when the investigations of nerve endings in muscles were already being carried out by means of impregnations with gold chloride. But it was only with the introduction of vital staining of nerves with methylene blue (Ehrlich, 1886) that the investigation of nerve endings in all regions of the body was placed on a firm foundation.

The present work was done by myself according to this method and only partly by means of impregnations with gold chloride.

In the muscles of the frog the same groups of nerve fibres are distributed as in the other vertebrates:

(*a*) *Medullated nerve fibres.* These may be in the form of thick or thin fibres, depending apparently on the thickness of the myelin sheath. But, in any case, both kinds are continually encountered and Bremer, not without reason, has ascribed them to two different groups. With caution it may be admitted that both varieties of medullated fibres are provided with terminations which are not identical.

The fibres of both groups, still some distance away from their termination, divide into 2–3 and some times more branches. On reaching the muscle fibre, the terminal nerve fibres divide again more often into two branches, when they

frequently lose their myelin sheath and terminate in the form of a non-medullated fibre.

(*b*) *Non-medullated nerve fibres.* These are numerous. Some of them, as we have just mentioned, result from the division of medullated fibres, diverging from these latter at the nodes of Ranvier. The others come from far away and it is difficult to say whether they have any connection with the medullated fibres or not. At least, they form extensive plexuses covering a large area and are provided with terminations differing considerably from the terminations of medullated fibres.

These non-medullated nerves belong, in my opinion, to the cerebrospinal nervous system and should not be confounded with

(*c*) the non-medullated nerve fibres of the sympathetic system, which, as has been more or less precisely established, are connected with the blood and the lymphatic vessels.

I shall now endeavour to describe the endings of the mentioned fibres according to my personal observations.

TERMINATIONS OF THE MEDULLATED NERVE FIBRES

There are two kinds. Some lie below the sarcolemma (hypolemmally), others outside the sarcolemma (epilemmally). The first are undoubtedly the terminations of motor nerve fibres, the second, in all probability, belong to sensory nerve fibres.

The relations presented by the motor nerves are quite definitely established. Every nerve fibre, after dividing several times, loses its myelin sheath, the sheath of Schwann fuses with the sarcolemma of the muscle fibre, and the axis cylinder enters into this latter and with its ramifications places itself immediately under the sarcolemma, without penetrating into the depth of the muscle substance. For a long time these relations have been handed down as a tradition by all authors, but I think in this question it is necessary to make a reservation or even perhaps more—an essential correction. One frequently comes across the statement that there enters into the muscle fibre what is described as a naked axis cylinder in the shape of a thin thread or a bundle of thinnest fibrillae. This, however, is very doubtful. The axis cylinder is never naked. On the contrary, along the whole extent of the nerve fibre, it is covered with an extremely fine layer of protoplasm, which is easily detected in well fixed preparations.

The axis cylinder never loses this protoplasmic covering and, in my opinion, *both together enter the muscle fibre.*

It is very important, I think, to establish in this respect some definite point of view. This would save the investigators many an error. I personally strongly believe that the granular substance covering the ramifications of the nerve ending belongs really to this protoplasmic layer and not to the substance of the muscle fibre and that it must not be confounded with the sarcoplasm, as is done by some authors. As a distinguishing characteristic, I would

emphasise that its capability of staining vitally with methylene blue as well as of reducing gold chloride is much stronger than is that of the sarcoplasm of the muscle fibre.

If this is so, it must be admitted that Kühne was quite right in distinguishing between two parts in terminal ramifications, viz. (*a*) threads of the axis cylinder (Axialbaum) and (*b*) a "stroma" substance, the nature of which Kühne does not define.

Kühne's observations were confirmed by Feist in a most definite form. He worked according to the method of vital staining with methylene blue and he established, in agreement with Kühne, that in terminal ramifications of motor endings it is possible to distinguish quite clearly a central, smoothly contoured thread intensely stained by methylene blue, and a less coloured peripheral mass (stroma, Kühne). When the preparation was fixed with picro-carmine, the peripheral part lost its blue colour and acquired a yellow shade, while the central thread preserved its former tint.

Retzius also says that such a differentiation was observed by him many times during his investigations, but he ignored these observations, taking them for an artificial result of treating the preparations with ammonium picrate.

A. Dogiel describes similar relations in reptiles, offering for them, however, no explanation.

Huber and de Witt, who also worked with methylene blue, affirm, that if the nerve terminations are examined immediately after being stained, no structure can be detected in the terminal ramifications. All branches of the axis cylinder are of an even blue tint. However, if in some 10–15 minutes the preparation is again exposed to the air, i.e. if the cover glass is taken off, it is possible to see, on examining it again, a central thread in many terminal branches. In preparations fixed with the ammonium molybdate, it is also sometimes possible to observe the presence of a central thread, but more often the axis cylinder ramifications appear to be finely granular. Huber and de Witt suppose that the differentiation which they observed and described depends upon the time which elapsed between the staining and the fixing of the preparation and upon the fixative used.

Personally, I can express quite a definite opinion upon the subject from my own observations and in an affirmative sense. The investigation of nerve staining according to the method of vital staining with methylene blue leaves, in my opinion, no doubt as to the fact that the hypolemmal terminal ramification of the nerve ending in the muscle fibre consists of a thin thread (perhaps a bunch of fibrillae) situated in the central part, always smoothly outlined and capable of being intensely stained with methylene blue. This portion is, in the strictest sense of the word, a continuation of the axis cylinder of the nerve fibre. Along the periphery of this central thread runs a thin layer of plasm, which is also stainable with methylene blue so that the terminal ramifications assume the appearance of the seemingly thickened continuations

of the axis cylinder, but this peripheral portion of the terminal branches easily loses its staining and on being fixed with ammonium picrate becomes granular, the result being that the structure of the nerve ending stands out with complete prominence. The peripheral part of the nerve ramification consists of a substance capable of great expansion, and under some conditions of coagulation, and therefore varies in appearance under the microscope, being sometimes homogeneous, sometimes granular, the latter condition appearing always in fixed preparations, and at the same time the terminal ramifications acquire characteristic varicosities owing to the change in the peripheral layer. The central thread invariably remains thin and smooth. The nuclei situated along the terminal threads (the so-called "noyaux de l'arborisation," Ranvier) belong to the peripheral (plasmic) part of these latter.

Let us now pass to the distribution of the terminal ramifications under the sarcolemma of the muscle fibre, i.e. to the external form of the nerve endings. They are very characteristic in the frog. In this respect, the muscles

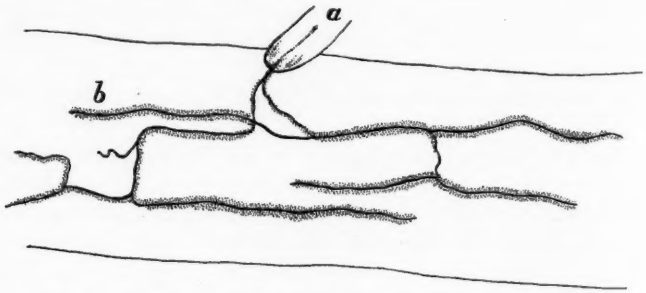

Fig. 1. Nerve ending in muscle fibre of frog; Methylene blue; *a.* medullated nerve fibre; *b.* ramifications of axis cylinders.

of Amphibia in general present a peculiar exception to all the rest of the Vertebrates. It has long since been established, that the axis cylinder of the nerve fibre immediately under the sarcolemma divides dichotomously, sometimes once, but mostly several times and that the terminal threads place themselves along the length of the muscle fibre. There are cases where the terminal threads are comparatively short, but more often they have the appearance of long branches, so that the nerve ending, which occupies a considerable portion of the muscle fibre, acquires its characteristic appearance, in marked contrast to the round or ovalish plates in other classes of Vertebrates.

Fig. 1 shows a typical form of the terminations in question. The axis cylinder of the nerve fibre, approaching the muscle fibre, divides into two branches. Then each branch in its turn divides 2–3 times. Each of the branches after the first division, however, forms already quite an independent little tree, the branches of which never anastomose with each other nor with the branches of the other tree. In this connection, I need only point out that

all the observations of anastomoses between the branches of terminal ramifications are thought, by the authors themselves, to be more or less doubtful and are in evident need of confirmation. I myself have never seen any such anastomoses. The drawing given is quite accurate. All the branches are

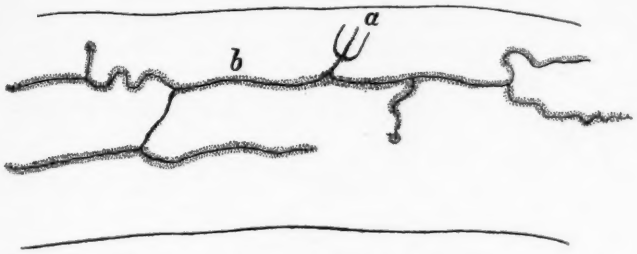

Fig. 2. Nerve ending in muscle fibre of frog; Methylene blue; *a.* medullated nerve fibre; *b.* ramifications of axis cylinders.

indicated, including their distribution, and actual form. There are nowhere any interruptions or varicosities. I consider that also in life the terminal threads of the nerve endings have this or a similar appearance. The varicose shape of the terminal threads, so characteristic of all kinds of nerve endings, is in my opinion an artificial product, which appears as the first sign of the approaching post mortem changes or as the result of the methods of histological investigation generally employed.

Figs. 2 and 3 show the same kind of hypolemmal terminations, with the slight difference that some terminal threads give out short sprouts, ending with leaf-like enlargements (fig. 2). Sometimes these sprouts divide and then,

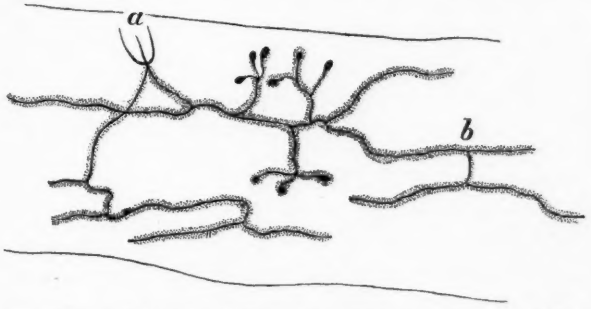

Fig. 3. Nerve ending in muscle fibre of frog; Methylene blue; *a.* medullated nerve fibre; *b.* ramifications of axis cylinders.

together with the leaf-like enlargements, they have the appearance of little bushes (fig. 3).

The ramifications of the terminal threads in question (*das Geweih* of German authors), preserving their character of ramifying threads stretched along the

muscle fibre, present a variety of small deviations the forms of which are well known and do not require detailed description. But when Huber and de Witt say that generally "a further description seems superfluous," this should be taken "cum grano salis." As regards all questions concerning nerve terminations in muscles, even cardinal questions, we are far from possessing the precise data which would give us the right to finish with them once and for ever. Therefore I venture to draw the reader's attention to a few of these varieties.

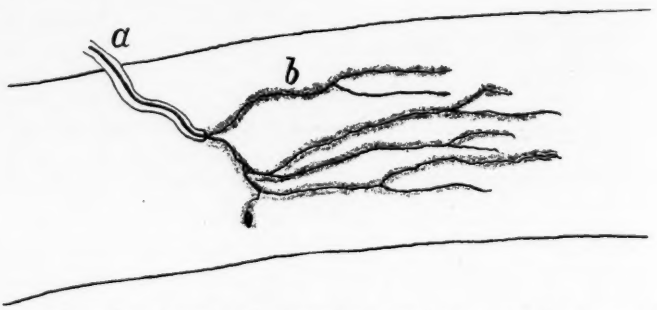

Fig. 4. Nerve ending in muscle fibre of frog; Methylene blue; *a.* medullated nerve fibre; *b.* ramifications of axis cylinders.

In one type, represented in figs. 4 and 5, the hypolemmal ramifications of the axis cylinder still present their usual character of long dichotomously dividing threads, but these latter do not place themselves along the extent of the muscle fibre, but, on the contrary, run across their length, and this difference is striking. We see it in figs. 7–8.

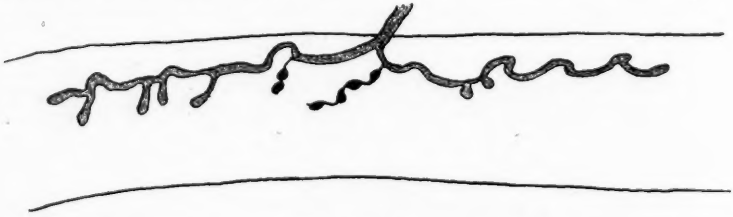

Fig. 5. Peculiar form of nerve ending in muscle fibre of frog; Methylene blue vital staining.

I should like to point out another very characteristic form which is very frequently encountered when the nerve termination is situated at the end of the muscle fibre. Usually, from the point of entrance of the nerve fibre into the muscle fibre, the terminal ramifications run along the extent of the muscle fibre both ways, as seen in figs. 1–3. At the ends of the muscle fibre it is possible to find, however, forms in which all the ramifications of the terminal threads direct themselves from the point of entrance of the nerve fibre towards the one side (fig. 4) and, if these ramifications are sufficiently numerous,

they occupy the entire periphery of the muscle fibre. In this case the impression is that the end of the muscle fibre lies as it were in a basket-like plexus of nerve threads. Finally, I also met with forms which are difficult to place under any of the above mentioned groups. In fig. 5, we see how, from the point of entrance of the nerve fibre, thick branches run along the muscle fibre, from which similar sprouts arise, very short, sometimes taking the shape of hooks. Such endings have also been observed by other authors, cf. Kühne, fig. 70*e*. It is difficult to decide whether this is a special form of ending or only an anomaly or some phase of physiological state.

In concluding the description of the hypolemmal nerve endings, I think it necessary to point out, that I have only described those that are numerous enough to be regarded as permanent forms. The forms that are rare, or found singly, I omit, as these are either anomalous or may owe their aberrant character to the methods employed.

Some authors (A. Dogiel) touch on the question of whether each fibre receives only one motor nerve termination or several and whether it is supplied from only one *bunch* of motor nerves or from different ones. In this respect A. Dogiel expresses himself more definitely than others. He holds that the muscle fibre may be supplied with one, two or three terminal nerve apparatuses and in cases where the muscle fibre has only the one nerve apparatus this latter, he points out, is often of a compound kind, i.e. it consists of several ramifying terminal branches. In cases where the muscle fibre receives several (2–3) terminal nerve apparatuses one of them is usually compound, while the others appear in a simpler form.

The above description, however, is not quite adequate. Under the name of the terminal nerve apparatus must be included the whole of the axis cylinder ramifications which enter into the muscle fibre, for example the nerve fibre, approaching the place of its termination, usually divides once or twice, as mentioned above, and enters into the muscle fibre with two or four axis cylinders, which ramify under its sarcolemma, but in doing so they form one terminal nerve motor apparatus. There are cases where the medullated nerve fibre runs for some distance along the muscle fibre and gives off to it fine branches arising from the nodes of Ranvier; then eventually its axis cylinder enters in the same way as the branches into the muscle fibre (fig. 6). As a result we have a strongly developed terminal apparatus, but still only one and not several. A. Dogiel himself affirms, that in the case where the muscle fibre is supplied with several terminal nerve apparatuses *only one nerve fibre, which divides, as shown above, into* 2–3 *branches*, takes part in their formation.

I have met many times in the frog strongly developed terminal apparatuses. One of them is shown in fig. 7. The nerve fibre before termination divides into two branches, both of which, having lost their medullary sheath, enter into the muscle fibre and form, under its sarcolemma, extensive ramifications. These occupy the whole extent of the muscle fibre, but they still form one

terminal apparatus. It seems to me that it would be an advantage if this point of view were accepted and if it were thus established that *every muscle fibre is supplied with only one terminal apparatus.*

This conclusion is not in conformity with the observations made by A. Dogiel, according to which the muscle fibre may receive its nerve apparatuses not from one nerve fibre only, but from various fibres approaching the muscle fibre from different sides. Such observations, however, are very doubtful as his

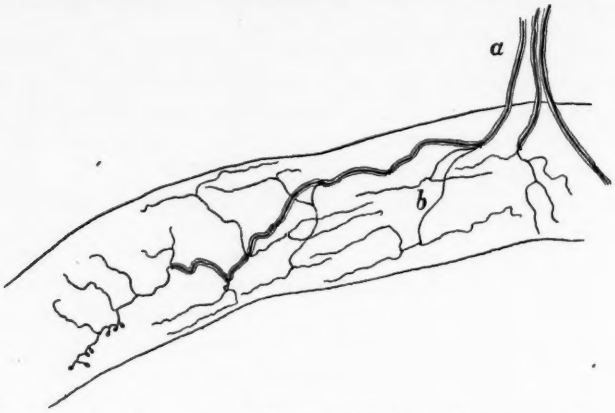

Fig. 6. Nerve ending in muscle fibre of frog; Methylene blue; *a.* nerve fibres; *b.* ramifications of axis cylinders.

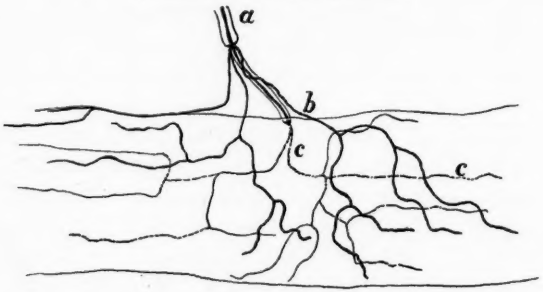

Fig. 7. Nerve ending in muscle fibre of frog; *a.* medullated nerve fibre; *b., c.* ramifications of axis cylinders.

fig. 7 is not convincing. In that figure, both nerve fibres approaching the muscle fibre are broken and it is difficult to judge whether they are independent fibres or whether they are branches of a single fibre artificially separated at the moment of preparation. I have an analogous preparation. It is shown in fig. 8. We see two muscle fibres *A* and *B*, supplied by a medullated fibre *a*, which divides into two branches. One, thinner, terminates in the muscle fibre *A*, in the terminal ramifications of its axis cylinder. The thicker branch passes towards the muscle fibre *B*. Before entering the muscle fibre it, in its

turn, divides into two branches, which terminate in fibre *B*, but one of these gives off a very thin branch *C*, which terminates in the muscle fibre *A*. If in our preparation we had encountered only one muscle fibre *A*, we should have concluded that it received two terminal nerve apparatuses from different nerve fibres, approaching from opposite sides, a conclusion which would have been incorrect.

This concludes my observations concerning the endings of the medullated nerve fibres of a motor character and I shall pass on to the description of sensory nerve terminations, but first I think it may be interesting to quote some references from histological literature.

Up to 1898 the question of nerve terminations in muscles, in spite of a colossal number of investigations, was in a distinctly unsatisfactory state.

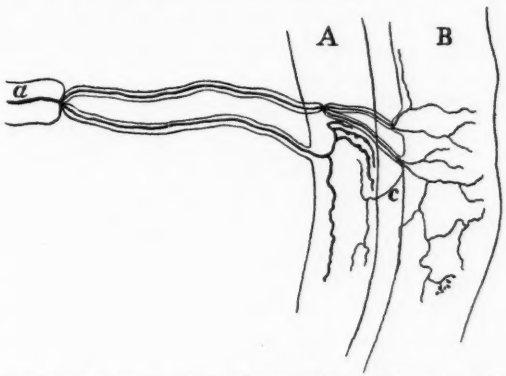

Fig. 8. Two nerve endings in muscle fibres of frog; gold chloride; *a.* medullated nerve fibre; *A.* and *B.* muscle fibres; *c.* additional nerve branch to muscle *A*.

A series of prominent investigators had described a great number of nerve terminations, very often quite precisely, but had given them such contradictory interpretations, that the whole question was left in a state of confusion. Such prominent observers as Kühne, Retzius, and A. Dogiel, accepted all the forms of nerve terminations in muscles, which they described, as being *motor* (hypolemmal) and only those of them that would not fit the established conception were distinguished by the name of "*atypical nerve endings.*"

Several of such atypical endings were described by Retzius in his classical work *Biologische Untersuchungen.* These forms were found by Retzius in the eye muscles of the rabbit and were regarded by him as motor terminations.

Retzius worked with methylene blue and his splendid drawings leave no doubt whatever of the fact that he made a very valuable observation and described the really original forms of nerve terminations.

In 1898, Retzius' observations were confirmed by Huber, but not in their entirety. Careful investigation of the nerve terminations in question brought Huber to the conviction that he was not examining the "*atypical forms*" *of*

motor terminations, but the normal forms of sensory nerve terminations. Huber, besides, established the fact that these terminations lie outside the sarcolemma (epilemmally).

Huber's work, in my opinion, was of immense importance and established a new line of advance for the study of this difficult question, for we find that very shortly after Huber's work there followed a series of investigations which presented the question of nerve endings from a totally different point of view and opened out a region of sensory nerve terminations, which had been for long completely ignored. Such are the works of Crevatin, Ceccherelli, A. Dogiel, and others. I hope to return to these works later on when I investigate the nerve endings in the muscles of the Mammalia. Here I shall endeavour to describe the sensory nerve terminations in the muscles of the frog and to establish that even if the motor terminations in the frog's muscles stand somewhat apart from those of other Vertebrates, the sensory nerve terminations essentially resemble those in all the higher Vertebrates.

TERMINATIONS OF THE SENSORY NERVE FIBRES

In the frog we find the sensory nerve endings connected with medullated nerve fibres, as well as with non-medullated. It is clear, of course, that some of the non-medullated fibres are branches of medullated fibres. This is often the case, but it would be very difficult to accept it as a rule for all cases. The non-medullated fibres often run quite separately from the medullated and are distributed in places where there are no medullated fibres at all. Besides, the non-medullated fibres often form considerable plexuses, in which the medullated fibres usually do not participate. It is, however, hardly possible to affirm at the present time that the non-medullated fibres form an entirely independent system of fibres. Here I refer only to those sensory fibres, which terminate either upon the surface of the muscle fibres or in the interstitial connective tissue, and not to the vaso-motor nerve fibres.

The medullated nerve fibres of the sensory nerves run in bundles, always independently of the motor fibres, but, like the latter, they cross the bundles of muscle fibres in a transverse direction and gradually give off short, often ramifying, non-medullated threads at the nodes of Ranvier. These threads terminate with leaf-like expansions. In rare cases the terminal threads give

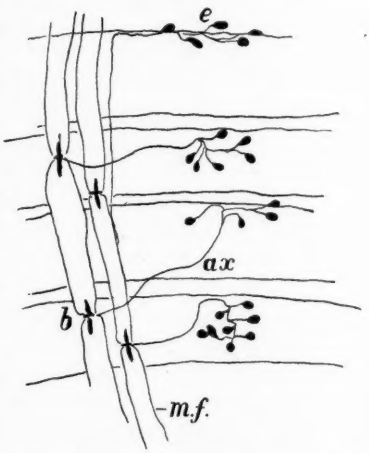

Fig. 9. Sensory nerve endings in muscle fibres of frog; Methylene blue; *ax.* axis cylinder; *m.f.* medullated nerve fibres; *b.* node of Ranvier; *e.* nerve endings.

off only 2–3 little branches. In the majority of cases the terminal thread splits into several branches each of which divides again. In such a case there would be quite a number of the leaf-like expansions. A nerve termination, whether large or small, always places itself on the surface of the muscle fibre, appearing in the shape of a plate, if examined from the side (in profile), but its real composition from threads with their leaf-like expansions always shows very clearly when it is examined from the surface (fig. 9). I should also point out that I possess preparations which indicate that the non-medullated threads given off from the medullated nerve fibre may be of a considerable

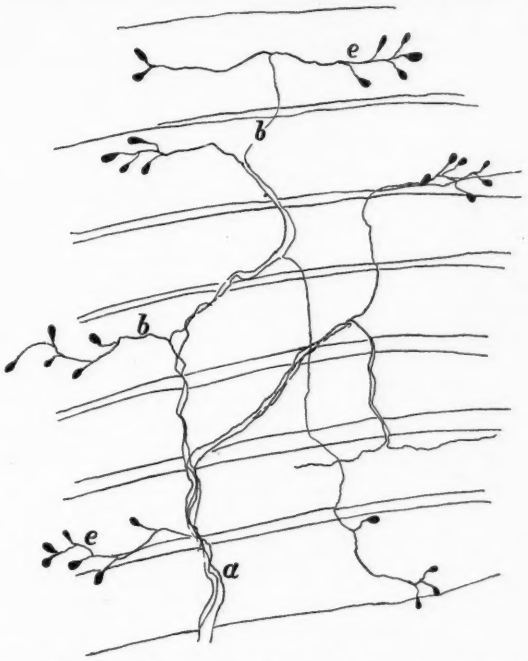

Fig. 10. Plexus of non-medullated nerve fibres in muscle of frog; Methylene blue; *a.* bundle of non-medullated nerve fibres; *b.* axis cylinders; *e.* nerve endings.

length. These terminate in the same way as the short threads, i.e. in a bush of ramifying threads with leaf-like expansions at their ends.

Fig. 10 shows the extensive ramifications of the non-medullated nerve fibres. These fibres may have sprung from medullated fibres, but in the preparation figured they have no connection with these latter. The principal branches also are evidently situated in a position more or less at right angles to the length of the muscle fibres, but fine branches and separate fibres run in the interstitial tissue along the muscle fibres for a considerable extent, as is seen in figs. 11–14.

Usually the bundles of non-medullated fibres, situated between the muscle fibres, preserve for the whole of their length a straight direction and curve only very slightly, but it often happens that they wrap over the muscle fibre and then they present a peculiar appearance, especially if the muscle is in a state of contraction (figs. 12, 13).

Here I must mention that the fibres in question were observed by Retzius in the eye muscles of the frog, but he took them to be motor fibres.

As to the terminations of the non-medullated nerve fibres, these are in principle everywhere similar and remind one of the already described terminations of the sensory fibres, derived from medullated fibres. The terminal

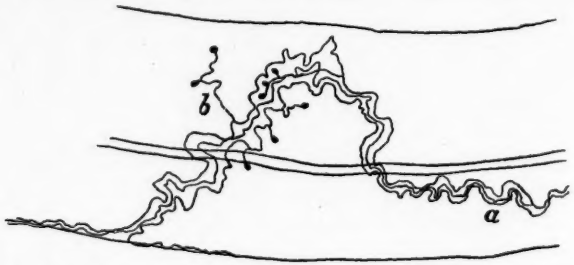

Fig. 11. *a.* Bundle of non-medullated nerve fibres in the interstitial tissue between the muscle fibres of frog; *b.* axis cylinders and their endings; Methylene blue.

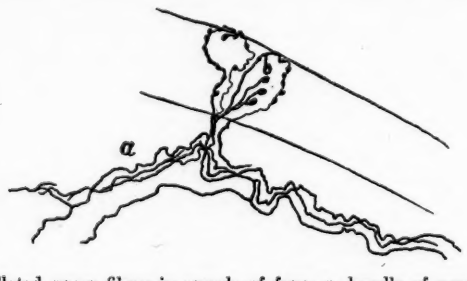

Fig. 12. Non-medullated nerve fibres in muscle of frog; *a.* bundle of non-medullated fibres; *b.* axis cylinders with their endings.

threads arise from the nerve bunch along the whole extent of the nerve fibre in the form of side sprouts, which terminate with leaf-like expansions. If the terminal threads have several ramifications, each one of the latter terminates with a leaf-like expansion and then the nerve termination acquires the appearance of a more or less considerable bush, but if it places itself upon the surface of the sarcolemma of the muscle fibre it acquires the shape of a plate. In individual cases, however, it is possible to come across a variety of forms in the described terminations.

In fig. 11 we see a characteristic bundle of non-medullated fibres, from which single short branches arise and terminate in leaf-like expansions. This

is the simplest form of termination. The leaf-like expansions may touch the muscle fibre.

We find almost the same thing in fig. 12. The only difference lies in the

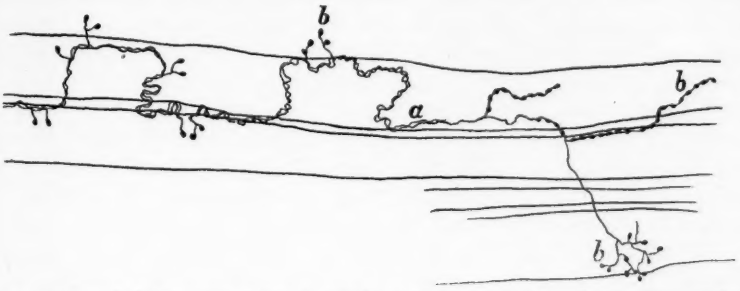

Fig. 13. Non-medullated nerve fibres in muscle of frog; *a.* nerve bundle; *b.* nerve endings; Methylene blue.

fact that here the nerve fibres wrap round the muscle fibre in the form of a fine bundle.

In fig. 13, the bundle of non-medullated fibres encircles the muscle fibre. From its fibres, the lateral terminal branches (*a*) arise, they divide dichotomously, and terminate in leaf-like expansions (*b*).

Fig. 14 shows a peculiar form. Along the muscle fibre a bundle of non-medullated nerve fibres is situated from which arise the side threads in a transverse direction, slightly ramifying. Each branch terminates in a leaf-like expansion with small terminal bushes. This form of termination was observed by Huber and Crevatin in the muscles of the eye in Mammalia. Fig. 14 very nearly approaches Crevatin's drawing.

I have taken for description only a few examples of these terminations. I do not attach any great importance to the forms described as such, as the principle in all these cases is the same.

Here I shall venture to leave the subject and to refer to the supposed special forms of nerve terminations, described for the first time by Giacomini under the name of nerve plexuses or "*terminaisons en réticelles.*" Unfortunately I am unable to refer to the papers of Giacomini and am only acquainted with them from the summary of Renaut et Regaut in the *Revue Générale d'Histologie* which seems to me to be excellent. The terminations "en réticelles" represent, according to Giacomini, the plexuses of thin non-medullated fibres round single muscle fibres or round small

Fig. 14. Non-medullated nerve fibres in muscle of frog; *a.* nerve bundle; *b.* axis cylinders and their endings.

muscular groups. In the *Revue Générale d'Histologie*, Crevatin's fig. 30 is reproduced, evidently corresponding to the description of these terminations by Giacomini. From the thin and varicose threads arise short side branches, which terminate in free expansions (par des extrémités libres renflées). It seems to me that the terminations "en réticelles," which Giacomini described quite correctly as sensory terminations, were observed long before his investigations, but were incorrectly interpreted. So we find them illustrated by Retzius (1892) and even by Bremer (1882). Both authors observed them in the adult frog. The terminations of Giacomini (en réticelles), I think, correspond altogether to the description of the sensory terminations in the muscles of the eye in Mammalia (A. Dogiel, Crevatin) and to my present description of the sensory terminations in the muscles of the frog (figs. 11, 14). But I should not like to call them "terminaisons en réticelles." The fact is, that the non-medullated bundles, which give origin to this kind of termination, sometimes have an external likeness to plexuses. They sometimes encircle the muscle fibre with several rings, but they do not form any real plexuses.

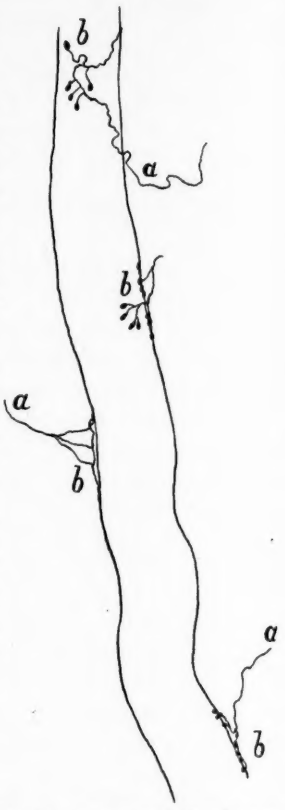

Fig. 15. *a.* non-medullated nerve fibres; *b.* axis cylinders with their endings; Methylene blue; frog.

It has been established by many authors that the muscle fibres are supplied with several sensory terminations. This is easily seen by observing the nerve fibres of the fine nerve bundles, which run along the extent of the muscle fibre and from time to time give off to it their terminal threads ending, as we saw above, in enlarged terminations or small bushes. I once succeeded in observing a muscle fibre which was supplied along a comparatively short distance with four plates of the typical form of sensory nerve terminations and, as I show in fig. 15, the terminations belonged not to one but to various nerve fibres. All the forms of sensory nerve terminations described by myself are, in my opinion, connected with muscle fibres. As I described above they all lie on the sarcolemma of the muscle fibre (epilemmally) and have neither granular lining nor nuclei. As to the structure of the said terminations, an important reservation is necessary. It is generally stated that the terminal thread whether short or long coming off from the fibre at the node of Ranvier erminates in an expansion. This is observed through the microscope under comparatively low powers. In preparations stained by the method of vital

staining with methylene blue such terminal threads appear to be thin, straight, and more or less intensively coloured blue. The idea of former authors was that they represent naked axis cylinders, but if they are examined under a sufficiently high power ($\frac{1}{12}$ oil-imm.), it is not difficult to become convinced that the structure of the nerve endings is more complicated and that the terminal thread is covered by an extremely thin layer of a plasmatic substance unstained by methylene blue (in fixed preparations).

I do not think that all the sensory nerve terminations are immediately connected with the muscle fibres. Some of them probably terminate in the interstitial connective tissue. It is however very difficult to make a definite statement, perhaps for the reason that the form of termination of the terminal thread is most likely the same, i.e. the terminal threads terminate either in separate leaf-like expansions or in small bundles. In any case, I have not observed here those characteristic relations which I have described in the muscles of snakes (*Journ. of Anat.* LVIII.). Besides the non-medullated fibres, which I have described, and which I ascribe, probably in accordance with other authors, to the cerebrospinal nervous system, it is not difficult to observe in the muscles of the frog extensive plexuses of thin fibres connected with the blood vessels of all sizes, not excepting the capillaries. At the places where the nerve staining with methylene blue was sufficiently intense, relations are observed, which leave almost no doubt that these plexuses participate in the innervation of the muscle fibres. We know that this kind of nerve fibre belongs to the sympathetic system and it would be most desirable to throw some light on their relations to the muscle fibres from the morphological point of view, but this is not easy to effect. The fact is that the sympathetic nerves may not have the definite apparatuses in which the nerves of the cerebrospinal nervous system terminate, but that they may terminate in peculiar plexuses similar to those described by Perroncito and which personally I have sometimes seen in the muscles of the frog, although not in such a definite form.

SUMMARY

1. In respect of their nerve terminations, frogs form no exception to the rule, and in their muscles the same groups of nerve fibres are distributed as in the other vertebrates, i.e. the medullated and non-medullated fibres of the cerebrospinal nervous system and sympathetic fibres.

2. The motor nerve terminations lie under the sarcolemma (hypolemmally), the sensory on the outside (epilemmally). The old dispute about where the nerve terminations of the muscle fibres terminate is thus solved in a sufficiently satisfactory way.

3. The nerve threads entering the muscle fibre do not simply represent the so-called naked axis cylinders of the nerve fibre but are enclosed in a layer of plasmatic substance, which forms the peripheral part of the terminal thread. This plasmatic part of the terminal thread should not be confused with the sarcoplasma of the muscle fibre. The significance of the plasmatic part

is perhaps analogous to that of the granular substance (sole) of the motor nerves in Lizards, Birds, and Mammalia.

4. The distribution of the terminal threads of the motor nerve in the muscle fibre of the frog is very characteristic. The terminal threads have the appearance of long fibres, usually dichotomously branched, running chiefly along the length of the muscle fibre, although terminations are encountered in which the terminal threads take other directions.

5. Each muscle fibre receives only one more or less complex motor nerve termination. One nerve fibre only participates in its formation. This latter, on dividing, may certainly supply with nerve terminations a considerable group of muscle fibres.

6. The nerve terminations which were described by Kühne, Retzius and A. Dogiel as "atypical" forms of motor terminations should be ascribed to the sensory nerve endings, as was first pointed out by Huber.

7. The sensory nerve terminations of the spinal nerves in the frog fully correspond to similar terminations in Mammalia. All forms of such terminations in these latter described by authors are very clearly observable in the frog.

8. In the frog *medullated* as well as *non-medullated* fibres terminate in sensory nerve endings.

9. In its essence, every sensory termination presents a thin terminal thread terminating with a leaf-like expansion. If the terminal thread is ramifying or gives off side sprouts, the termination becomes more complicated and appears in the shape of a nerve apparatus more often having the appearance of a plate lying with its expansions upon the sarcolemma. The sensory nerve terminations, whether they belong to medullated or non-medullated nerve fibres, have all essentially the same constitution.

10. The muscle fibre may be supplied with several sensory nerve terminations.

11. It is very possible that the structure of the sensory nerve apparatuses is more complicated than is described by authors at the present time. There is reason to conclude that the terminal threads of these terminations, as well as those of the motor, are enveloped in plasmatic substance.

12. It must be held that part of the non-medullated nerve fibres terminate in the interstitial connective tissue.

In a subsequent paper, I hope to deal with the sympathetic nerve endings in the muscles of the frog.

The present work has been carried out thanks to the assistance of the Medical Research Council, to which I feel it my duty to express my deep gratitude.

I wish also to avail myself of this opportunity to express my heartfelt thanks to the Professors of University College—Prof. G. Elliot-Smith and Prof. J. P. Hill—for their invariably friendly consideration for myself and my work.

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THE ABDOMINAL DISTRIBUTION OF THE VAGUS

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In the course of some work on the influence of the vagi nerves on the functions of the stomach, it was found necessary to obtain an accurate knowledge of their anatomical distribution in the abdomen, and this paper is the outcome of the investigation.

The course and distribution of the vagi nerves to the oesophagus and to the intra-abdominal organs are given in very general terms and brief space in the present-day text-books of anatomy. The literature reveals many varying statements as to the arrangement and manner of distribution of their branches in the sub-diaphragmatic region, whilst the structure of the oesophageal plexus as shown by earlier observers has been neglected. In any account of the sub-diaphragmatic distribution of the vagi, it is necessary to consider the influence of the structure of the oesophageal plexus on this distribution.

Perman summarises the differences found by various workers, the principal being:

1. The number of nerve stems passing through the oesophageal opening of the diaphragm.
2. The presence or absence of an anterior and posterior gastric plexus.
3. The presence or absence of a subserous gangliform plexus.

He himself, writing in 1916, denies the presence of any subserous ganglia and has never found either an anterior or a posterior gastric plexus.

The work of most interest and importance is found in the writings of Swan, Bourgery, Kollmann, Perman and Latarjet.

Swan (1834) gives an interesting account of the distribution of the vagi nerves, illustrated by very beautiful plates. He states that about the lower part of the oesophagus the vagi form the oesophageal plexus; from this two trunks are derived passing through the oesophageal opening of the diaphragm, one lying anteriorly and the other posteriorly. Three branches of the right vagus together with one from the left form the posterior trunk; the anterior trunk is formed by the union of two branches of the left vagus with one from the right. Further he describes a communication from the left to the right vagus about the level of the roots of the lungs.

The posterior trunk supplies filaments to the cardia, some of which communicate with similar twigs from the anterior division; branches are then supplied to the posterior aspect of the stomach. A branch to the splenic plexus is noted; also communications with twigs of the anterior trunk on the

left gastric artery and with branches of the right hepatic plexus on the right gastric artery, these nerves being then distributed to the stomach. Communications with branches of the coeliac plexus about the left gastric artery are referred to. The nerve is described as terminating in the coeliac plexus. The anterior trunk supplies branches to the cardia, some of these communicating with twigs of the posterior trunk as noted above. Several branches pass to the left hepatic plexus. The main branches follow the lesser curvature of the stomach and are distributed to the anterior aspect of this organ; some run with the left gastric artery to meet on this artery branches of the right hepatic plexus as well as filaments from the posterior trunk.

The hepatic branches are figured as passing to the porta hepatis between the layers of the lesser omentum. The plates show an anterior gastric plexus.

Bourgery (1844) shows the anterior trunk divided into three stems and, as such, passing through the diaphragm: these are formed from several branches of the left vagus and one from the right. The posterior trunk, derived from three branches of the right vagus and four of the left, is broken up at the oesophageal opening into numerous divisions. A plexiform mass is figured. The stems of the posterior trunk are distributed to the posterior aspect of the stomach and to the coeliac ganglia. Communications between branches of the anterior and posterior trunks are to be seen on the lesser curvature, but no posterior gastric plexus is shown.

The stems of the anterior trunk give hepatic branches, a branch to the pyloric region, and branches to the anterior aspect of the stomach.

Communications with the sympathetic about the left gastric artery are shown. He names, but does not illustrate, an anterior gastric plexus.

Kollmann (1860) observed that both vagi form about the lower oesophagus the oesophageal plexus and that, near the oesophageal opening of the diaphragm, branches from this form two main stems, one lying anteriorly and one posteriorly; each stem contains fibres of both vagi. He noted that in the cat and rabbit the plexus maintains a constant relation and he describes the arrangement in the dog.

An anterior and a posterior gastric plexus are described. No plexuses are found in the rabbit, cat or dog, though some connections exist.

The anterior stem passes through the diaphragm in two or three branches, and forms on the cardia the anterior gastric plexus; this varies in size and may be absent. Branches pass to the liver through the lesser omentum, these and the main branches to the anterior surface of the stomach are described. Branches pass to the pylorus and form connections with the sympathetic fibres about the *left* gastric artery; together they supply this region.

The sympathetic nerves to the anterior surface of the stomach were examined in fifteen cases: in four, branches were found passing to the left of the oesophagus to reach the anterior stomach wall, these being derived from the left coeliac plexus or from the sympathetic plexus about the left inferior phrenic artery. In one case, Kollmann found communications between these fibres and vagal fibres, and in three cases branches passed through the lesser omentum to the liver without joining the vagal gastric branches. The posterior stem, having passed the diaphragm, gives about one-third of its fibres to the posterior aspect of the stomach; these communicate with sympathetic twigs to form the posterior gastric plexus, which, like the anterior, varies in size and may be absent.

Branches are only distributed over the proximal half of the posterior

surface, the distal third receiving sympathetic fibres from the plexus about the left gastric artery. The remaining two-thirds of the stem pass to the coeliac plexus and through its connections to the liver, pancreas, spleen, kidneys, suprarenals and small intestine.

Perman (1916) gives an exhaustive review of the literature up to the time of his work, but does not refer to that of Swan. His own work is especially concerned with the distribution of the branches of the vagi to the stomach; these he describes in detail. He has never observed the presence of either an anterior or posterior gastric plexus as described by many others, although he notes some small communications on the lesser curvature between the branches of the anterior and posterior vagal trunks. He believes that the ganglia lying under the serosa and described by Openchowski, Worobjew and Muller, as well as others, are merely those of Auerbach's plexus appearing through defects in the longitudinal muscle coat.

Latarjet (1921) and his co-workers have of recent years investigated the distribution of the vagi to the stomach and liver. Their findings for dog and man are similar; the anterior trunk (left vagus) supplies four or five branches to the stomach, the main branch following the lesser curvature to reach and supply the pyloric antrum; the posterior trunk (right vagus) also gives off rami which run with sympathetic twigs to the porta hepatis. The pylorus is supplied from above by fine twigs (supra-pyloric nerves), which run a recurrent course in the lesser omentum and are derived from the nerves to the liver; the latter fibres are mainly if not entirely sympathetic. The posterior trunk sends a stem to the coeliac plexus. They point out that the "stomach reservoir" and the pylorus differ in the manner of their nerve supply. Plexus formation was not observed.

Sympathetic fibres reach the liver as described above and such fibres also reach the stomach; they follow the left gastric artery along the lesser curvature and anastomose with vagal twigs. Other sympathetic fibres run with the right gastro-epiploic artery and supply a few sparse twigs to the stomach along the greater curvature; they are derived from the nerves about the hepatic artery.

It will be seen from the literature that some of the earlier workers have described and figured the structure of the oesophageal plexus; of late years it is usual to find only brief references to a plexus about the lower third of the oesophagus. Swan figured and described the conformation of the plexus, and later Kollmann described it, emphasising that both vagi nerves supply fibres to both surfaces of the stomach. Duccheschi, quoted by Cannon, has observed that one cervical vagus can innervate the whole stomach. As regards the number of trunks passing through the oesophageal opening of the diaphragm, descriptions vary. Swan shows a single anterior and a single posterior stem; Bourgery figures multiple anterior branches, as do Henle and Spalteholz: Bourgery figures also multiple posterior: Kollmann states that the anterior trunk is divided into two or three branches whilst the posterior apparently remains single: Perman shows the anterior either single or divided into two, the posterior single. Again, the presence of an anterior and posterior gastric plexus is in doubt; amongst those describing these plexuses are Swan, Bourgery, Kollmann, Luschka, Henle, Schwalbe, Hollstein, Jonnesco and Spalteholz:

they have not been described by Sappey, Schafer and Symington in Quain's *Anatomy*, and Perman amongst others. The statement of Kollmann that they are variable in size and may be absent would appear to reconcile these observations, but Perman in 1916 could find neither plexus present in dissections of twenty specimens. Many workers in describing these plexuses, limit their formation to the gastric branches proper; some have described all branches as taking part in their formation.

The accounts of the distribution of the branches of the anterior trunk to the liver are not without conflicting statements; most authors agree that a branch or branches from the anterior trunk pass to the porta hepatis, crossing high up between the layers of the lesser omentum. Whether nerves pass along the lesser curvature and then proximally from the pyloric region is more doubtful; Valentine has described the latter twigs. Others state that the main vagal branches do not reach the distal portion of the stomach. It follows from the last statement that there exists a divergence of opinion as to the manner in which the pylorus is innervated. Kollmann describes branches of the anterior stem passing along the lesser curvature to the pylorus and thence proceeding to the first stage of the duodenum. Sappey also described these. Latarjet attributes the supply of the pylorus exclusively to the hepatic nerves derived from the coeliac plexus; Swan also figures such twigs.

It is to be noted that Kollmann, with Henle and Luschka, states that the posterior trunk only supplies the proximal part of the posterior surface of the stomach, the remainder receiving sympathetic twigs; the majority of workers however describe all this surface as receiving twigs from the posterior stem. The descriptions given of the abdominal distribution of the posterior trunk, other than to the stomach, are meagre. A full discussion of the literature is to be found in the article by Perman.

METHOD

Specimens for dissection were prepared according to the method described by Perman, which is an elaboration of that of Woolridge.

1. The tissues are immersed in acetic acid 1 per cent. for 24 hours.
2. They are washed and placed in carbolic acid 6 per cent. for from 20 to 40 minutes.
3. They are again washed and then preserved in a saturated watery solution of picric acid; after 24 hours in this they are ready for dissection.

Prepared in this manner the specimens are soft and pliable and the nerves are easily recognised as white glistening strands. Specimens keep indefinitely in the picric acid solution, but it must be borne in mind that the penetrative action is not great and that the larger organs, such as the liver, may undergo central autolysis.

The terminology used follows the B.N.A., and as regards the parts of the stomach the description given in Cunningham's *Text-Book of Anatomy* is followed.

Dissections were made of six infants, aged three to nine months, and in one boy of fifteen years. The following account is compiled from these; minor individual variations occur and are referred to in the descriptions of the individual specimens.

DISSECTION OF THE VAGUS

Both vagi, having passed posterior to the lung roots, incline anteriorly and medially and proceed to divide, the right usually into three branches, sometimes four, the left almost invariably into three. These branches are

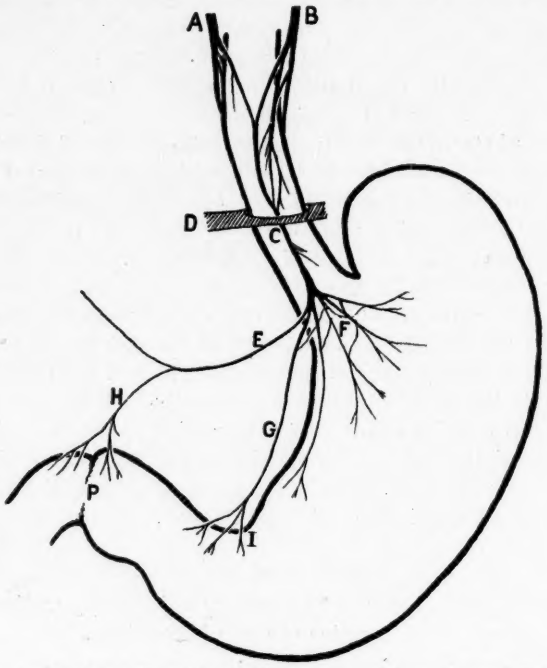


Fig. 1. Drawing made from a dissection showing the normal formation and distribution of the anterior vagal trunk. *A*, right vagus. *B*, left vagus. *C*, anterior vagal trunk. *E*, hepatic branch. *F*, gastric branches. *G*, principal anterior nerve of the lesser curvature. *H*, branches to pylorus and first stage of the duodenum. *P* indicates the position of the pylorus; *I*, that of the incisura angularis, and *D* the diaphragm.

then arranged about the lower third of the oesophagus in the following manner: two branches of the left nerve pass to the anterior aspect of the oesophagus and there unite with one branch of the right which has also reached this aspect; the latter branch is small as compared with the remaining divisions of the right nerve. Together these nerves form a very simple plexus on the anterior surface of the oesophagus, and from this one or two stems pass through the oesophageal opening of the diaphragm, forming the anterior vagal trunk.

The remaining divisions of the right and left nerves, in number usually two or three of the right and one of the left, have by now passed to the posterior aspect of the oesophagus and there form a plexus, again simple, from which there usually arises a single trunk, the posterior vagal trunk, passing through the oesophageal opening of the diaphragm.

The oesophagus is supplied by numerous fine twigs which arise from these various nerve stems as they lie closely applied to its wall. Intercommuni-

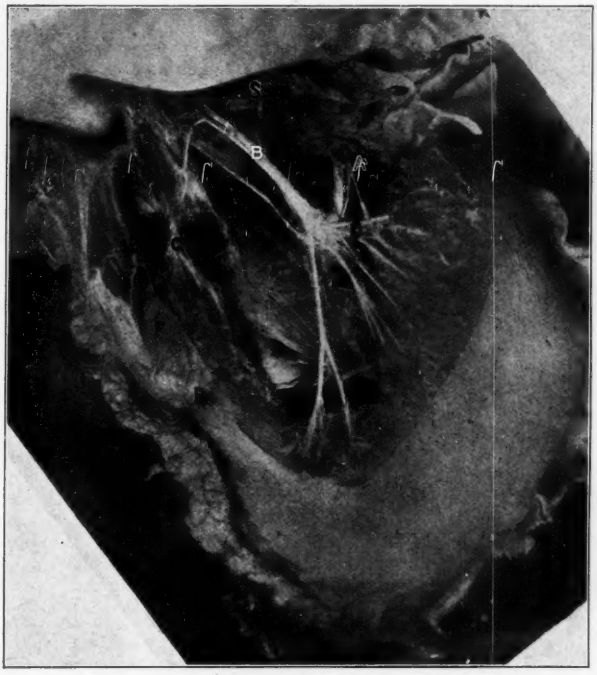


Fig. 1 A. Photograph of a dissection of the anterior vaga trunk and its branches in a child aged three months. *A*, anterior vagal trunk (two stems) on the lower oesophagus. *B*, hepatic branches. *C*, pyloric nerves (vagal and sympathetic). *D*, cardiac and gastric branches. *E*, principal anterior nerve of the lesser curvature. *P* indicates the porta hepatis; *S*, the caudate or Spigelian lobe of the liver; *F* is placed on the first stage of the duodenum, and *R* on the pylorus.

cations between the main stems of the anterior group are found and between the stems of the posterior group, varying in number, and with their number the plexus varies in complexity. The oesophageal plexus is therefore seen to be composed of an anterior and a posterior group of nerves.

The anterior vagal trunk (fig. 1), having passed through the oesophageal opening as one or two stems, supplies several fine twigs to the lower end of

the oesophagus and to the cardia; it then breaks up into its main branches, in most cases from three to six in number. These may be divided into two groups, a group lying to the right and on an anterior plane usually consisting of two stems, and a group to the left and on a deeper plane of three to four stems.

The left group may or may not show interconnections, few or many in number, in the latter case an anterior gastric plexus is formed. Its main branches of distribution associate themselves with the anterior branches of the left gastric artery, and supply the region of the anterior surface of the cardia, fundus and proximal portion of the body of the stomach. Some communications are also always present with the right group of branches. The right group gives origin to three main branches of distribution; the first passes out into the lesser omentum and proceeds towards the porta hepatis, its manner of termination being described below. The second, a large nerve, passes down between the layers of the lesser omentum, a short distance from, and parallel to, the lesser curvature of the stomach; it is distributed to the anterior surface of the pyloric antrum and body of the stomach in the neighbourhood of the incisura angularis, but does not reach the pyloric canal. The third branch lies on and follows the lesser curvature along the line of attachment of the lesser omentum; it is to be traced in most cases to the incisura angularis. These last two are, in most instances, reinforced by fibres from the left group of branches. Communications to the coeliac plexus from the branches of the anterior vagal trunk are present, passing proximally with the left gastric artery. One or two communications are received from branches of the posterior trunk on the lesser curvature in the region of the cardia. That branch of the right group proceeding towards the porta hepatis is frequently duplicated; its terminal twigs are divided into two series, a proximal which can be traced into the porta hepatis, and a distal turning downwards, from which twigs pass (*a*) to the pylorus and first stage of the duodenum, (*b*) to run with the right gastric artery, and thus to the region of the pyloric canal, (*c*) to run deep to the pylorus and first stage of the duodenum with the gastro-duodenal artery and so towards the head of the pancreas and second stage of the duodenum, (*d*) to run proximally on the wall of the hepatic artery, and (*e*) to communicate with sympathetic twigs passing to the gall-bladder. Those fibres running on the walls of the right gastric, gastro-duodenal and hepatic arteries soon become lost amongst sympathetic twigs, and in many cases they may be observed to communicate with these.

The posterior vagal trunk (fig. 2) in most cases a single stem, supplies fine twigs to the lower oesophagus and cardia, the lowest of which is of some size and constancy. It then divides shortly after passing through the oesophageal opening into two main divisions: of these the smaller is destined for the stomach, the larger for the coeliac and other abdominal sympathetic plexuses.

That portion for the stomach gives off first fine twigs to the lower oesophagus and cardia, one of which, distributed to the posterior aspect of the

cardia, is of some size and constancy. A branch then passes for a short and variable distance along the lesser curvature and sends twigs, in most cases two, to communicate with branches of the anterior vagal trunk. A common method of termination of the gastric stem is that in which a branch is given off to the posterior aspect of the proximal portion of the body; the stem then continues in the falciform ligament and gives off three branches for the supply of the posterior surface of the body and pyloric antrum, these at their terminations associating themselves with the branches of the left gastric artery. The

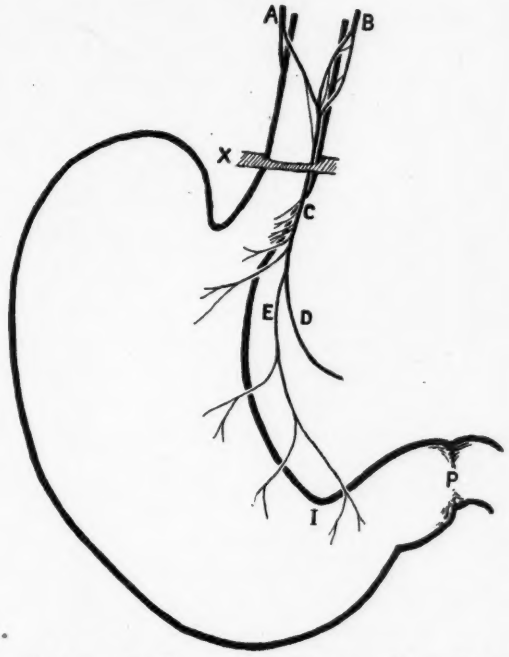


Fig. 2. Drawing made from a dissection illustrating the normal formation and distribution of the posterior vagal trunk. The stomach has been turned to the right, exposing the posterior surface. *A*, left vagus. *B*, right vagus. *C*, posterior vagal trunk. *D*, coeliac division. *E*, gastric division, which lies in the coronary falx. *P* indicates the position of the pylorus; *I*, that of the incisura angularis, and *X* the diaphragm.

most distal of them is distributed in the neighbourhood of the incisura angularis, but does not reach the pyloric canal.

As with the anterior vagal trunk a plexus, the posterior gastric plexus, may or may not be formed. When present, it is confined to the gastric divisions of the trunk. The major portion of the posterior vagal trunk associates itself with the stem of the left gastric artery and passes proximally. It supplies fibres to both right and left coeliac ganglia. Other fibres may be traced directly on to the splenic artery and to the pancreas and some, anastomosed with

sympathetic fibres, run with the superior mesenteric artery and hepatic artery and to the renal and suprarenal plexuses.

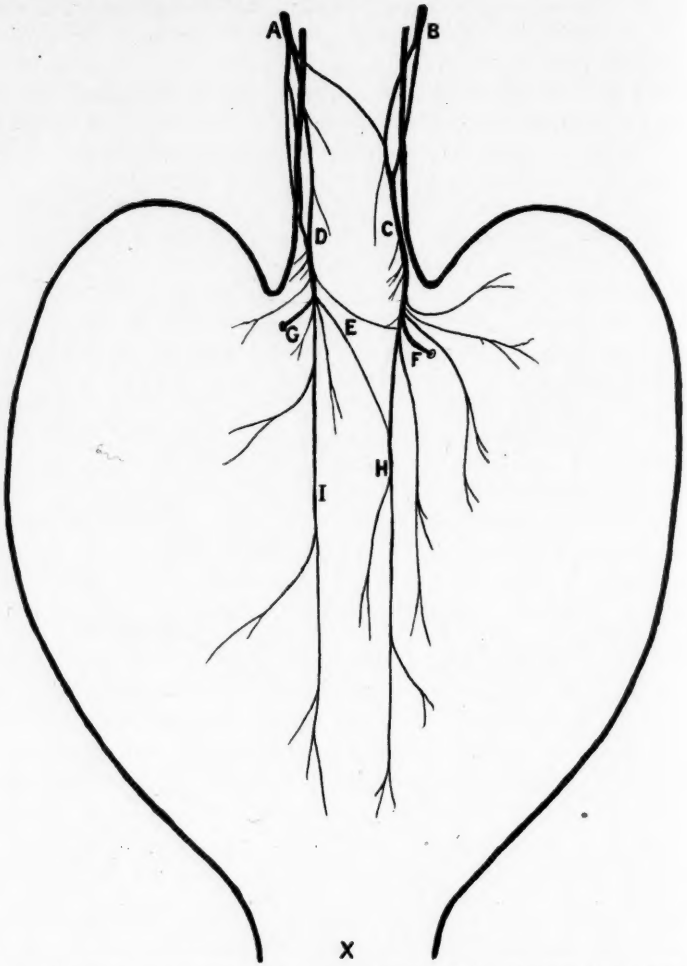


Fig. 3. Drawing made from a dissection to illustrate the distribution of the anterior and posterior vagal trunks. The stomach has been opened along the line of the greater curvature. *A*, right vagus. *B*, left vagus. *C*, anterior vagal trunk. *D*, posterior vagal trunk. *E*, communications on cardia between anterior and posterior vagal trunks. *F*, hepatic ramus. *G*, coeliac ramus. *H*, principal anterior nerve of the lesser curvature. *I*, principal posterior nerve of the lesser curvature. *X*, pylorus.

It is a matter of considerable difficulty to determine whether these last fibres are vagal or sympathetic or both, on account of their intricacy and of the manner in which the nerves are matted together.

A note on the origin and manner of distribution of the sympathetic fibres to the stomach is perhaps not out of place. This supply is entirely derived from the coeliac plexus.

These nerves are grouped as follows:

(*a*) Fibres from the coeliac plexus pass with the left inferior phrenic artery and so to the stomach; they wind about the anterior aspect of the lower extremity of the oesophagus from left to right, communicate with branches of the anterior vagal trunk and are distributed to the region of the cardia and fundus.

(*b*) Fibres pass with the left gastric artery from the coeliac plexus, and may be divided into three groups:—(1) Passing with the oesophageal and superior branches of this artery to the cardia and proximal part of the body of the stomach; reinforcements are received from the fibres with the right inferior phrenic artery. These twigs may be traced to the cardia and to communicate with branches of the anterior and posterior vagal trunks. (2) Fibres which pass with the main stem of the artery along the lesser curvature to supply both surfaces of the body of the stomach and pyloric antrum; one branch lying closely applied to the lesser curvature is of considerable size. (3) Fibres passing across between the layers of the lesser omentum towards the porta hepatis, communicating with the hepatic branches of the anterior vagal trunk in the majority of instances.

(*c*) Fibres pass from the coeliac plexus along the hepatic artery; these form several large nerves and are distributed with its branches; they reach the pyloric region of the stomach with the right gastric and right gastro-epiploic arteries.

Group (*b*) is much the most prominent and supplies the major portion of the stomach.

DISSECTION I. Female infant, aged 3½ months.

The oesophageal plexus: the left vagus divides into three main branches, the right into four. Two of those from the left nerve unite together with the smallest of the right to form the anterior vagal trunk, which passes through the oesophageal opening as a single trunk. The remaining branch of the left joins together with three of the right to form the posterior vagal trunk, passing through the oesophageal opening as a single stem. All these branches supply fine twigs to the oesophagus.

The anterior vagal trunk, having passed through the diaphragm, supplies numerous fine twigs to the lower oesophagus and cardia. It then divides into (1) a single hepatic ramus, passing out between the layers of the lesser omentum to the porta hepatis, and (2) four larger branches which pass to supply the stomach, no anterior gastric plexus being formed; the hepatic ramus was not followed further. The largest of the gastric branches lies in the lesser omentum and follows the lesser curvature as far as the region of the pyloric antrum; it is reinforced in the neighbourhood of the cardia by a small branch from the posterior vagal trunk.

The posterior vagal trunk divides into two portions, the larger passing towards the coeliac plexus along the trunk of the left gastric artery, the smaller to the stomach.

The latter branch supplies fine twigs to the lower oesophagus and cardia and also two small twigs which wind about the cardia to join branches of the anterior vagal trunk. Two main branches of the gastric division are then found passing along the lesser curvature deep to the plane of attachment of the lesser omentum; the proximal supplies the proximal portion of the posterior surface of the body of the stomach, whilst two to three branches

from the more distal supply the remainder of the posterior surface of the body and pyloric antrum.

No posterior gastric plexus is present.

Dissection II. Female infant, 6 months.

The oesophageal plexus: the left vagus divides into three branches, two of these unite together with one smaller branch of the right vagus on the anterior aspect of the oesophagus to form the anterior vagal trunk; this passes through the oesophageal opening of the diaphragm as a single stem. The right divides into three main branches: the smallest (as seen above) unites with the branches of the left vagus to form the anterior trunk, the remaining two together with the third branch of the left vagus, noted above, unite to form the posterior vagal trunk on the posterior surface of the oesophagus; this again passes through the oesophageal opening as a single trunk. All branches supply fine twigs to the oesophagus. Minor divisions of these branches exist accentuating the plexiform arrangement. The anterior vagal trunk, having supplied several small twigs to the oesophagus and cardia, breaks up on the anterior aspect of the cardia into at first three and later five main branches.

The two lying to the left and on a deeper plane form the anterior gastric plexus lying on the cardia and supplying branches to the cardia, fundus and body of the stomach; a branch passes in the lesser omentum along the lesser curvature of the stomach to the region of the incisura angularis. The two lying to the right and on a more superficial plane are distributed as follows: one follows the lesser curvature to the pyloric antrum; the other passes out between the layers of the lesser omentum to the liver, this branch communicates with the sympathetic fibres from the coeliac plexus which run with the right inferior phrenic and left gastric arteries. A branch from the deep division of the anterior vagal trunk also passes in the lesser omentum to the liver and is reinforced by a twig from the posterior vagal trunk. A third hepatic twig crossing in the lesser omentum is derived from the sympathetic plexus about the left gastric artery. From these branches which pass between the layers of the lesser omentum towards the liver, twigs may be traced into the porta hepatis, to the pylorus, and to unite with sympathetic fibres passing to the gall bladder; others run downwards posterior to the pylorus to pass with the gastro-duodenal artery towards the head of the pancreas and second stage of the duodenum, while yet others accompany the hepatic artery, passing proximally towards the coeliac plexus.

The posterior vagal trunk divides into two groups of branches, the smaller for the stomach, the larger for the coeliac and other sympathetic plexuses.

The branches for the stomach consist of several small oesophageal and cardiac branches, one of which is of some size. The remaining stem runs in the left gastro-pancreatic fold and gives off three branches for the supply of the posterior surface of the stomach and pyloric antrum; the most distal of these is distributed in the neighbourhood of the incisura angularis, but does not reach the pyloric canal.

No posterior gastric plexus is present.

The larger division of the posterior vagal trunk associates itself with the stem of the left gastric artery; two chief branches were identified entering the coeliac ganglia to the right and the left of the aorta. Twigs continued directly on to the splenic artery and into the substance of the pancreas, those on the splenic artery being finally lost amongst sympathetic fibres.

Dissection III. Female infant, 5 months (fig. 4).

Oesophageal plexus: the left vagus divides into three main branches, the right also into three, of which one is smaller than the remaining two. The last, together with two branches of the left nerve forms the anterior vagal trunk which passes through the diaphragm in the form of two stems lying close together. The posterior vagal trunk, a single stem, is formed by the union of one branch of the left vagus with two larger divisions of the right. All stems supply fine twigs to the oesophagus and this structural arrangement is complicated by smaller connections between the stems forming each trunk.

The two stems composing the anterior vagal trunk, having supplied twigs to the lower oesophagus and to the cardia, divide up on the anterior aspect of the cardia; the branches may be separated into two divisions, a right and a left. The left division supplies twigs to the fundus and proximal portion of the body and sends communications to the right group. The right division supplies four chief branches, the first passing out between the layers of the lesser omentum towards the liver; the second follows the lesser curvature lying in the lesser omentum, receives a communication from the left division and gives off, near its

origin, a branch which passes out in the lesser omentum and supplies the pylorus from above (fig. 4); it then terminates just proximal to the incisura angularis. Of the remaining two branches, one passes almost transversely to the left, being distributed to the proximal part of the body, the other lies deep and follows the lesser curvature; it may be traced almost to the incisura angularis.

An anterior gastric plexus is present, mainly formed by the branches of the left division. A deep branch passes back from the right division towards the coeliac plexus, along the trunk of the left gastric artery. Two communicating branches from the posterior vagal trunk are received in the region of the cardia.

The branch to the liver divides in the neighbourhood of the porta hepatis into two, the superior enters the liver, the inferior passes downwards and supplies twigs to the pylorus and first stage of the duodenum, while others run with the right gastric and hepatic arteries.

The posterior vagal trunk supplies fine twigs to the lower oesophagus and cardia, the lowest of which is a branch of some size; it then divides into two main divisions, a smaller gastric and a larger one which passes to the coeliac and other abdominal plexuses.

The gastric division gives off three principal branches; firstly one which passes along the lesser curvature for a short distance and anastomoses with branches of the anterior vagal trunk; secondly one which passes to supply the proximal part of the posterior surface of the stomach; the third branch divides into three twigs which reach the remainder of the posterior surface of the body, and the lowest of which reaches the incisura angularis and terminates on the posterior aspect of the pyloric antrum. These branches associate themselves with the posterior branches of the left gastric artery.

All these nerves are at their origins interconnected by an extremely fine and complex network of nerves, the posterior gastric plexus. The major division passes along the trunk of the left gastric artery to the coeliac ganglia in which it mainly terminates; other fibres however accompany the splenic artery.

Dissection IV. Male infant, 5 months.

Oesophageal plexus: the left vagus divides into three branches, the right into four. These are arranged in the usual manner; two from the left nerve and one from the right form the anterior vagal trunk; three of the right and one of the left the posterior vagal trunk. The anterior trunk passes through the oesophageal opening of the diaphragm as a single stem, the posterior trunk in the form of two stems.

The anterior vagal trunk supplies fine twigs to the oesophagus and cardia and three branches to the fundus and proximal part of the body of the stomach; one branch follows the lesser curvature lying in the lesser omentum, supplies twigs to the body and terminates in the region of the incisura angularis, its terminal twigs reaching the pyloric antrum. An hepatic ramus is given off in the usual manner; this breaks up as it lies between the layers of the lesser omentum and becomes intermingled with sympathetic fibres. It gives off twigs to the porta hepatis and others which descend to the pylorus and first stage of the duodenum, whilst yet others run with the right gastric artery and with the hepatic artery. No anterior gastric plexus is present.

The posterior vagal trunk supplies the lower oesophagus and cardia as in other specimens and sends, on the cardia, communicating twigs to the branches of the anterior trunk, in particular its hepatic ramus. Its two stems then divide into gastric and coeliac divisions, the two gastric unite and proceed as a single stem in the left gastro-pancreatic fold; this stem supplies three branches to the posterior surface of the stomach and terminates near the incisura angularis: it reaches the pyloric antrum. Before union of the gastric divisions, that of the left side supplies one branch to the proximal portion of the body and to the fundus. The coeliac divisions pass separately to become lost in the coeliac plexus. No posterior gastric plexus is present.

Dissection V. Male, aged 15 years (figs. 5, 6 and 7).

The oesophageal plexus possesses the customary basic structure; two branches of the left vagus together with one of the right form the anterior vagal trunk: two branches of the left nerve and two of the right form the posterior vagal trunk. Both vagal trunks pass as single nerves through the oesophageal opening of the diaphragm. The anterior vagal trunk breaks up on the anterior aspect of the cardia into four branches, the three lying to the left supply the anterior aspect of the cardia, fundus and body, that on the right gives

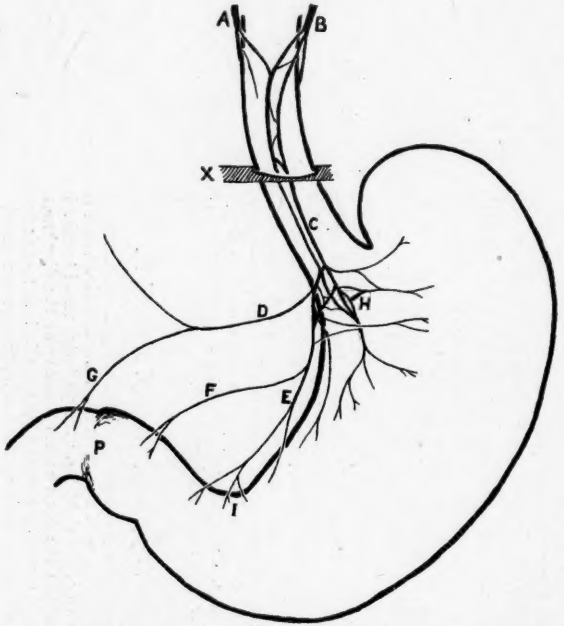


Fig. 4. Drawing made from Dissection III showing the vagal branch destined solely for the pylorus. *A*, right vagus. *B*, left vagus. *C*, anterior vagal trunk. *D*, hepatic branch. *E*, principal anterior nerve of the lesser curvature. *F*, branch to pylorus. *G*, branch to duodenum. *H*, gastric branches. *P* indicates the position of the pylorus; *I*, that of the incisura angularis, and *X* the diaphragm.

Fig. 5. Photograph of Dissection V, anterior aspect, illustrating the formation and distribution of the anterior vagal trunk. *A*, right vagus. *B*, left vagus (anterior branches). *C*, communication from right to left vagus. *D*, anterior vagal trunk. *E*, hepatic branches. *F*, descending branch to pylorus and first stage of the duodenum. *G*, gastric branches. *H*, principal anterior nerve of the lesser curvature. *L* is placed on the cut surface of the liver, the left lobe of which has been removed. *P* indicates the position of the pylorus.

which has been removed. *P* indicates the position of the pylorus.

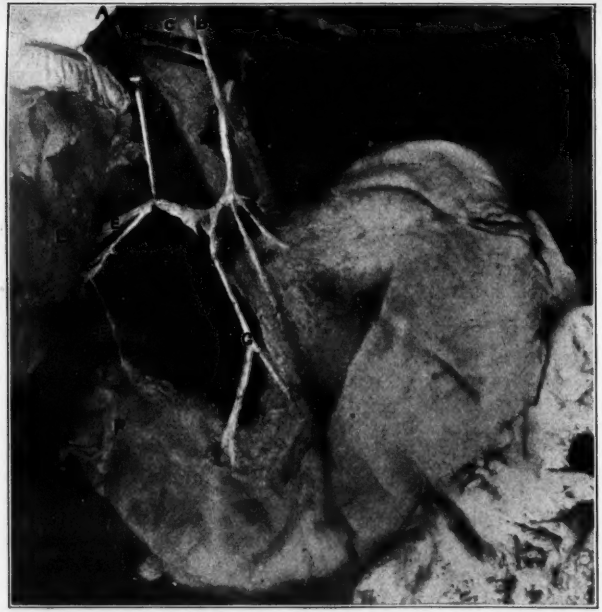


Fig. 6. Photograph of Dissection V, anterior aspect, illustrating the formation and distribution of the anterior vagal trunk. *A*, right vagus. *B*, left vagus (anterior branches). *C*, communication right to left vagus. *D*, anterior vagal trunk. *E*, hepatic branches. *F*, descending branch to pylorus and first stage of the duodenum. *G*, principal anterior nerve of the lesser curvature. *H*, gastric branches. *L* is placed on the cut surface of the liver, the left lobe of which has been removed; *P* indicates the position of the pylorus.

Fig. 7. Photograph of Dissection V, posterior aspect, illustrating the formation and distribution of the posterior vagal trunk. *A*, branches of left vagus. *B*, branches of right vagus. *C*, posterior vagal trunk. *D*, coeliac division. *E*, gastric division. *F*, principal posterior nerve of the lesser curvature. *P* indicates the position of the pylorus, and *X* the site of the incisura angularis.

origin to firstly, a large branch which lies in the lesser omentum and follows the lesser curvature, to be distributed in the neighbourhood of the incisura angularis; and secondly, branches to the liver, three in number, which form a plexiform arrangement in the lesser omentum. Pyloric twigs are derived from the lowest of these branches to the liver. The posterior vagal trunk supplies twigs in the normal manner to the lower oesophagus and to the cardia, the lowest of which is a branch of some size; the main trunk then divides into gastric and coeliac divisions. The gastric division runs in the left gastro-pancreatic fold and its continuation, the falciform ligament: it gives off two branches for the supply of the posterior surface of the body of the stomach and terminates in the region of the incisura angularis, some twigs reaching the pyloric antrum. The coeliac division passes mainly to the coeliac plexus; some twigs however pass onward together with sympathetic fibres. These were not followed further because of the intimate connections existing between them and the sympathetic fibres.

No anterior or posterior gastric plexus was present.

The remaining dissections differed in no essential detail from those described above.

The literature on the anatomy of the vagus in animals is scanty. The vagus of the rabbit, in particular the oesophageal plexus, is referred to by Kollmann. Krause briefly states that the left vagus supplies the anterior, the right the posterior surface of the stomach. Jacobi describes and figures with its variations the communications found between the two vagi nerves on the posterior surface of the oesophagus immediately proximal to the cardia: he mentions no other communications between the two nerves. In eight of ten dissections he found that the left vagus was mainly distributed to the small intestine; on stimulation, however, he found that in 17 out of 37 cases the left vagus acted mainly on the intestine, in 15 on the stomach and in 5 the action was approximately equal.

In the case of the cat Mivart states that the left vagus supplies the liver and ventral surface of the stomach, whilst the right supplies the dorsal surface and spleen. In addition to the note by this author, the only other reference I have found is a brief note by Kollmann on the oesophageal plexus.

The literature on the vagus of the dog is more extensive. Kollmann describes the structure of the oesophageal plexus and gives the branches of distribution: Ellenberger and Baum figure and describe the oesophageal plexus; they show the anterior trunk giving off hepatic rami as in man, whilst its terminal branches reach the pylorus: the posterior trunk is seen to terminate in the coeliac plexus. Latarjet states that the vagi are distributed in the dog as in man, the pylorus receiving its sole supply from the hepatic nerves.

Hartung has investigated the vagi of the sheep in their lower thoracic and abdominal course; he carefully describes the gastric and hepatic branches.

DISSECTIONS

The specimens were prepared for dissection in the same manner as described above for the human dissections. Twenty rabbits were dissected, twelve cats and six dogs. A description of the findings follows.

Rabbit (fig. 8).

The right and left vagi, having given off their pulmonary branches, communicate with one another ventral to the oesophagus. This communication, which occurs immediately

below the level of the roots of the lungs, usually takes one of two forms, but minor variations occur. The two main types are as follows:

(*a*) The more usual condition: a branch or branches of the right vagus pass to join the left nerve.

(*b*) Chiasma formation: the two nerve trunks unite into one for a short distance, then this divides again into two. Two trunks proceed distally from this plexus, both supplying twigs to the oesophagus, and having numerous intercommunications with one another. That on the right side soon passes dorsal to the oesophagus; that on the left passes down

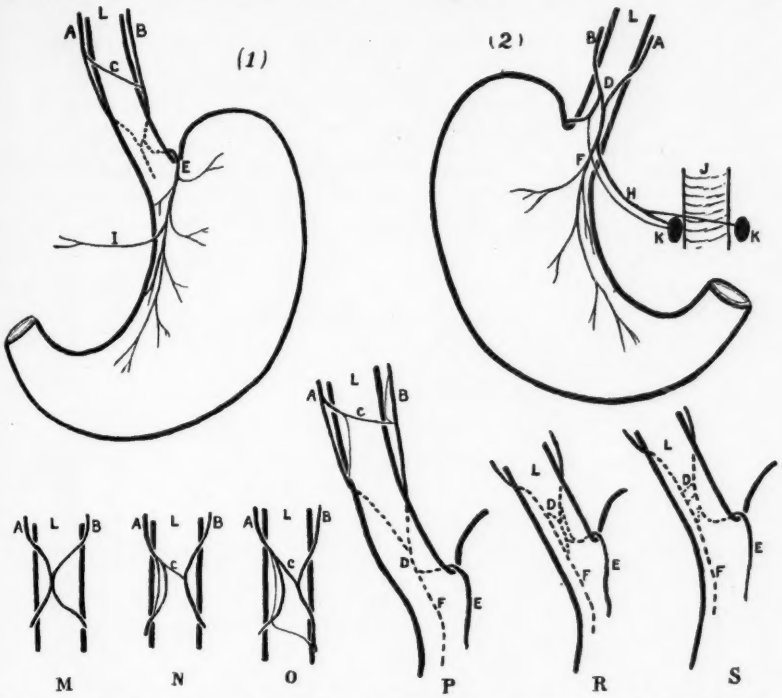


Fig. 8. Drawings illustrating the oesophageal plexus of the rabbit and the distribution of its branches, (1) anterior, (2) posterior. *A*, right vagus. *B*, left vagus. *C*, anterior communication between right and left vagi. *D*, posterior communications (supra-cardiac) between right and left vagi. *E*, anterior gastric vagus. *F*, posterior gastric vagus. *H*, coeliac division. *I*, hepatic branch. *J*, aorta. *K*, coeliac ganglia. *L*, oesophagus. *M*, *N*, *O* and *P* illustrate variations in the form of the anterior communication between the right and left vagi. *P*, *R* and *S* illustrate variations in the posterior (supra-cardiac) communications.

on the left of the oesophagus until, a short distance above the cardia, it also passes dorsally. Both trunks now unite on the dorsal aspect of the oesophagus immediately above the cardia; the manner and degree of union being most variable, ranging from a chiasma formation to that of two parallel trunks connected to one another by numerous delicate twigs. The most usual structure found is that in which one or two large twigs pass from the left to the right trunk, with in addition fine transverse communications. This formation together with two variants is figured above.

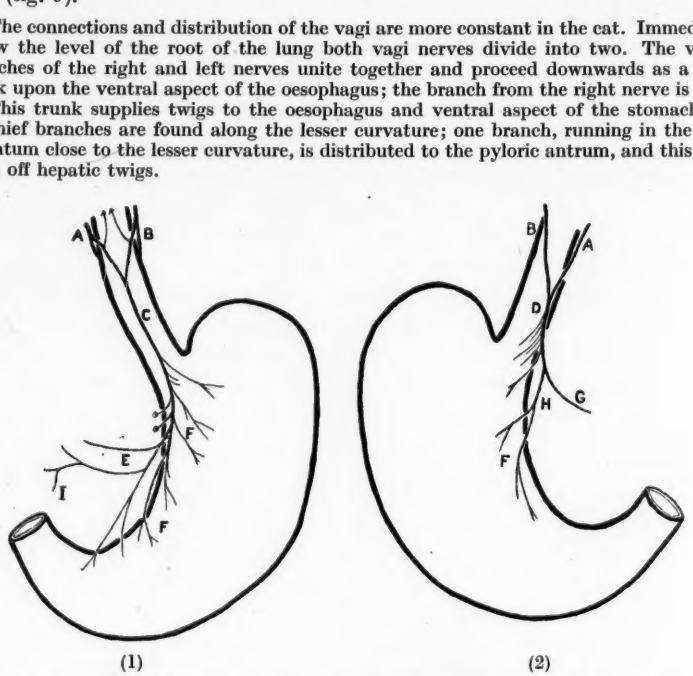
From this plexiform structure two main groups of branches arise, a right and a left. The left passes to the left and ventrally, winding about the lower extremity of the oesophagus to be distributed to the ventral surface of the stomach; the main branches run

along the lesser curvature and terminate in the pyloric antrum. One or more fine twigs arise proximally and pass out into the lesser omentum towards the liver. The right group passes dorsally and to the right supplying the dorsal surface of the stomach, while its main branches follow the lesser curvature to the pyloric antrum; in addition from this group there arise one or more nerves passing to the coeliac plexus. Both groups supply twigs to the cardia. The left group is also connected to the coeliac plexus either by a separate twig or by one combining with that of the right. The nerves do not form a plexus on the stomach wall.

CAT (fig. 9).

The connections and distribution of the vagi are more constant in the cat. Immediately below the level of the root of the lung both vagi nerves divide into two. The ventral branches of the right and left nerves unite together and proceed downwards as a single trunk upon the ventral aspect of the oesophagus; the branch from the right nerve is small.

This trunk supplies twigs to the oesophagus and ventral aspect of the stomach, and its chief branches are found along the lesser curvature; one branch, running in the lesser omentum close to the lesser curvature, is distributed to the pyloric antrum, and this nerve gives off hepatic twigs.



(1) (2)

Fig. 9. Drawings illustrating the formation and distribution of the anterior (ventral) and posterior (dorsal) vagal trunks in the cat. The anatomical arrangement in the dog is similar, (1) anterior, (2) posterior. *A*, right vagus. *B*, left vagus. *C*, anterior vagal trunk. *D*, posterior vagal trunk. *E*, hepatic branch. *F*, gastric branches. *G*, coeliac division. *H*, gastric division. *I*, pyloric branch.

The dorsal branches of the right and left nerves incline dorsally, supply twigs to the oesophagus and, at a point one to two centimetres proximal to the cardia, unite to form a single stem on the dorsal aspect of the oesophagus. This dorsal trunk is distributed to the dorsal surface of the stomach and to certain sympathetic plexuses and abdominal organs. The main branches of the gastric division are again found on the lesser curvature; they reach the stomach through the left gastro-pancreatic fold, one branch reaching the pyloric antrum. The second division arises about the level of the cardia and passes mainly to the coeliac plexus; twigs may however be traced directly accompanying the splenic, superior mesenteric and hepatic arteries, while others join the renal plexuses. The ventral trunk gives off proximally two or more fine twigs passing out into the lesser omentum towards the porta hepatis.

The nerves do not form a plexus on the stomach wall.

DOG.

A close resemblance is found to the cat. The vagi nerves divide to form ventral and dorsal trunks in a similar manner and position to that described above; the ventral branch of the right vagus is, as in the cat, considerably smaller than that of the left. The ventral trunk supplies the ventral surface of the stomach, sending its main branches along the lesser curvature between the layers of the lesser omentum; they may be traced to within 2 cm. of the pylorus. This trunk also gives off hepatic twigs, one or two in number; they pass high up in the lesser omentum to the liver and fine twigs from these pass downwards towards the pylorus. The dorsal trunk, as in the cat, divides into two; the gastric portion reaches the stomach through the left gastro-pancreatic fold and passes to within a short distance of the pylorus; its main branches lie along the lesser curvature. The second division gives off branches which may be traced to the coeliac plexus; others run with the superior mesenteric artery and splenic artery: the latter supply fine twigs which enter the pancreas.

Experiments were carried out in order to determine histologically whether fibres from each vagus nerve were distributed to both the anterior and posterior surfaces of the stomach, a mode of distribution strongly suggested by the macroscopic findings.

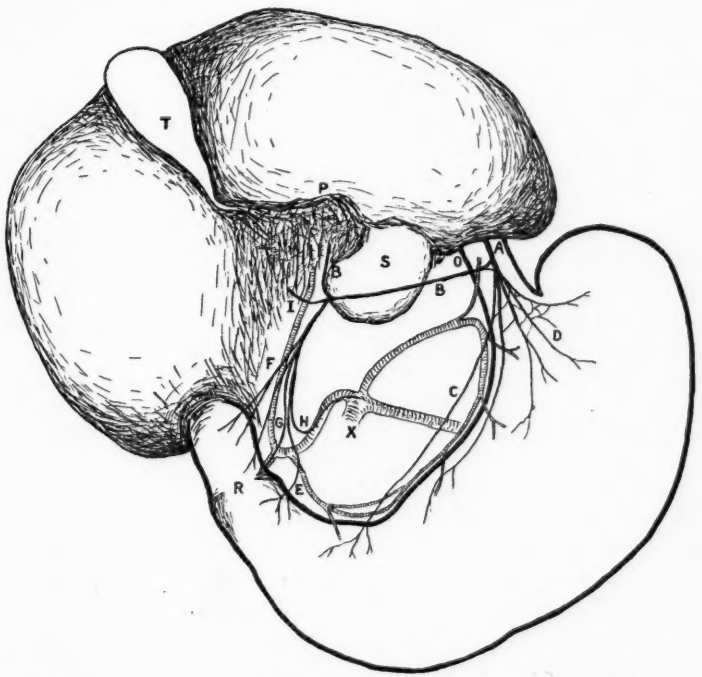


Fig. 10. Drawing to illustrate the distribution of the anterior vagal trunk. *A*, anterior vagal trunk. *B*, hepatic branch. *C*, principal anterior nerve of the lesser curvature. *D*, gastric branches. *E*, pyloric branch. *F*, duodenal branch. *G*, branch with gastro-duodenal artery. *H*, branch passing proximally on hepatic artery. *I*, branch to gall bladder. *X*, coeliac axis. *P*, porta hepatis. *S*, caudate lobe. *T*, gall bladder. *O*, oesophagus. *R*, pylorus.

Method

One vagus was divided, under aseptic conditions, in the cervical region of an animal, sufficient time was permitted to elapse to allow of the occurrence of degeneration of the nerve: the animal was then killed and sections of the vagi, of the anterior and posterior vagal trunks and of their branches were prepared and stained either by the Weigert method or by means of haematoxylin and Van Giesen. Four rabbits and two cats were used in these experiments.

The results fully confirmed the macroscopic findings and proved that each vagus nerve, through the oesophageal plexus, supplies fibres to both the anterior and posterior surfaces of the stomach.

Experimental stimulation of the vagi in the dog, cat and rabbit, has confirmed the statement of Ducceschi that either cervical vagus can innervate the whole stomach.

DISCUSSION

The results of this investigation on the distribution of the vagi nerves may be discussed under three headings: (1) the structure of the oesophageal plexus, (2) the branches and distribution of the anterior vagal trunk, and (3) the branches and distribution of the posterior vagal trunk.

(1) *The oesophageal plexus*

The descriptions of the general formation of the plexus given by Swan, Bourgery and Kollmann have been confirmed. It is important to note that the plexus possesses a most constant structural basis, which, as Kollmann stated, demonstrates definitely that each vagus supplies fibres to both the anterior and posterior surfaces of the stomach; the anterior and posterior vagal trunks formed from this plexus pass through the oesophageal opening of the diaphragm as single stems in the majority of cases: in none of my specimens was either trunk divided into more than two divisions. The descriptions found in the literature differ considerably as to the number of stems passing through the diaphragm, some even stating that the oesophageal plexus itself is continued through on to the cardia; it is probably rare to find more than two stems replacing either the anterior or posterior vagal trunk.

The structure of the oesophageal plexus in the cat and dog is essentially similar to that in man, though on a simplified scale. The description for the dog, given in the preceding pages, is similar to those of Kollmann, and Ellenberger and Baum. In the rabbit the structure of the plexus is seen to be somewhat different, but again each vagus is found to send fibres to both surfaces of the stomach; Jacobi's description of the oesophageal plexus of this animal is incomplete. It is interesting to note that the structure of the plexus in the sheep, as described by Hartung, closely resembles that of the rabbit.

(2) *The anterior vagal trunk*

The preceding findings are in general similar to those of Swan, Kollmann, Perman and Latarjet; some points however require discussion. The statement

of Kollmann that the anterior gastric plexus is variable and may be either present or absent is entirely confirmed and it is surprising that both Perman and Latarjet were unable to find such a plexus present. It is possible that individual observers differ widely as to the number of intercommunications necessary to constitute plexus formation; in some cases however one can have no hesitation in stating that a plexus is present, and in all instances at least one or two communications pass between neighbouring branches. The plexus, when present, is confined to those branches destined for the supply of the stomach; this statement is in accordance with the findings of the great majority of workers.

The anterior vagal trunk gives off one, sometimes two or three branches to the liver which cross to that organ in the lesser omentum. Swan and Kollmann show that these communicate with sympathetic fibres (the left hepatic plexus); the latter however noted a few cases in which he found these connections to be absent. Swan pictures twigs descending from this anastomosis to the pylorus and first stage of the duodenum: Latarjet states that the pylorus receives its entire nerve supply from above and believes them to be sympathetic, derived from nerves accompanying the hepatic artery (right hepatic plexus), and running a recurrent course in the lesser omentum. In my dissections such pyloric twigs are present and it would appear that certain of these are vagal in origin: in one case, Dissection III (fig. 4), a definite branch from the main branch of the anterior vagal trunk passes out into the lesser omentum and supplies the pylorus from above, without having any connection with sympathetic fibres or supplying a branch to the liver.

The main branch of the anterior vagal trunk lies between the two layers of the lesser omentum and follows the lesser curvature of the stomach. It reaches the region of the incisura angularis and its terminal twigs supply the pyloric antrum: in no case does this nerve send fibres as far as the pyloric canal or sphincter. Latarjet supports this view, but Kollmann and Perman, amongst many others, state that all the anterior surface of the pyloric region receives its nerve supply from this branch which runs along the lesser curvature. It may be noted that in the diagrams given by Perman this nerve terminates at some distance from the pylorus.

As regards the cat, dog and rabbit the findings are similar so far as the greater difficulties of dissection permit of accurate observation. The distribution follows the same plan but no plexus is ever present and Kollmann's observations support this: the main branches on the lesser curvature terminate in the pyloric antrum. Ellenberger and Baum, however, figure these in the dog proceeding to the pylorus, but Latarjet states that the pylorus, as in man, is supplied from above by the nerves of the liver.

(3) *The posterior vagal trunk*

The descriptions given by Perman and Latarjet of the gastric divisions are largely substantiated by my investigation. The statement of Kollmann

that a posterior gastric plexus may or may not be present is confirmed; if present it is confined to the gastric branches. This same worker finds that only the proximal half of the posterior surface of the stomach is supplied with vagal twigs: this is incorrect, for the nerves only fail to reach the pyloric canal and sphincter. The description given by Kollmann of the coeliac division is substantiated, although in the dissections of man it is difficult to differentiate between sympathetic and vagal fibres: in animals the vagal fibres are more distinct and can be traced out with greater ease. A point to emphasise is that the gastric division reaches the stomach by passing through the left gastro-pancreatic fold and its continuation, the falciform ligament; its branches do not lie in the lesser omentum. In the cat, dog and rabbit the distribution of the posterior vagal trunk is similar in its general plan; no posterior gastric plexus is ever present.

In general it may be stated that this investigation, except on a few points, confirms the work of Kollmann, whose work has not received due recognition in this country, and it is evident that, with the exception of the papers of Swan and Kollmann, no observer has attempted to give a full account of the course and manner of distribution of the vagi nerves in their lower thoracic and abdominal course[1]: the result of this has been that the importance of the influence of the oesophageal plexus on their distribution has been lost sight of.

The descriptions of the vagal distribution to the stomach given by Latarjet in his brief communications are exact and clear with the exception of one point—he does not state whether any vagal fibres reach the pylorus and one infers that the supply is entirely sympathetic. His nomenclature is useful, he names the main branch of the anterior trunk which passes along the lesser curvature "the principal anterior nerve of the lesser curvature," and the corresponding branch of the posterior trunk "the principal posterior nerve of the lesser curvature." These two nerves are conspicuous objects in any dissection.

Finally it must be noted that the descriptions of the oesophageal plexus as usually given are inaccurate and misleading, that the statement that the left vagus supplies the anterior surface of the stomach and the right the posterior, is incorrect, and that the variety of findings in regard to the anterior and posterior gastric plexuses depend on (*a*) their variability, and (*b*) the opinion of the individual observer as to what constitutes a plexus.

SUMMARY

1. The oesophageal plexus is in the structure and arrangement of its larger branches constant.

2. Two trunks arise from the oesophageal plexus, the anterior vagal trunk and the posterior vagal trunk; each trunk contains fibres of both left and right vagi nerves.

[1] I have been unable to refer to the paper of Dorello.

3. These vagal trunks in the majority of instances pass through the oesophageal opening of the diaphragm each in the form of one or two stems.

4. Anterior and posterior gastric plexuses may or may not be present: the one may be present, the other absent. If present, their formation is limited to the branches destined for the supply of the stomach.

5. The manner of distribution of the vagal branches is in the main constant.

6. The main gastric branches lie in the neighbourhood of the lesser curvature.

7. The anterior vagal trunk supplies the anterior surface of the stomach as far as the pyloric antrum; it does not supply the pyloric canal and sphincter through those branches which lie along the lesser curvature.

This statement holds good for the posterior vagal trunk and the posterior aspect of the stomach.

8. The pyloric canal, sphincter, and first stage of the duodenum receive their nerve supply from above, receiving twigs from the vagal branches to the liver.

9. Vagal branches may be traced in man to the liver, pancreas and coeliac plexus; in addition, in animals, fibres may be traced to the suprarenal and renal plexuses, and to run with the hepatic, splenic and superior mesenteric arteries.

10. Sympathetic fibres derived from the coeliac plexus reach all regions of the stomach, twigs may be seen to unite with and run with vagal twigs.

11. The oesophageal plexus of the cat, and dog follows the same plan as that of man.

12. Gastric plexuses are not found in the dog, cat or rabbit.

13. The distribution of the vagi in the abdomen of the cat, dog and rabbit is essentially similar to that of man.

14. The vagal twigs in these animals remain more distinct from sympathetic fibres than in man, and their distribution may be more accurately followed distal to the coeliac plexus.

I am indebted to Prof. J. S. B. Stopford for the drawings from my specimens and I desire to express to him and to Dr B. A. McSwiney my thanks for their aid and advice.

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AN ABNORMAL SKULL FROM NEW GUINEA, WITH REMARKS ON THE STRUCTURE OF THE MANDIBLE

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INTRODUCTION

There recently came into our hands, through the courtesy of Dr W. Simmons of Bexley, Sydney, N.S.W., four skulls from the mandated territory of New Guinea. One of these was so remarkable, even at first glance, that we decided to carefully describe it, as we considered it might throw some light upon the subject of bone growth. The outstanding feature of the skull is the marked thickening of the whole body of the mandible, especially in the region below the molar and premolar teeth. A feature which is even more remarkable, perhaps, though not so obvious at first glance, is the fact that the two remaining anterior teeth in the lower jaw actually have alveolar bone growing up, entering the root canal, and there expanding so as to retain these teeth in position. Further, nearly all the remaining teeth show marked shortening of their roots and corresponding shallowness of their root sockets. Nevertheless, the teeth appear perfectly healthy, in so far as any local disease is concerned. Attached to one of the zygomatic arches by some vegetable fibre, was the skull (minus mandible) of a dog. This abnormal human skull, with its remarkable mandible, is said to have come from the Madang district on the mainland of New Guinea (old German New Guinea). No further history is available.

DESCRIPTION OF THE MANDIBLE

The thickening of the body of the lower jaw is most marked in the molar and premolar regions, but continues forwards to the symphysis. The alveolus is not involved to any appreciable extent. For descriptive purposes, we will distinguish a right from a left sub-molar thickening, as well as an anterior enlargement. As a result of the thickening in the molar regions, the normal bracket-like projection of the alveolar arch in the region of the third molar, on the lingual aspect of the bone, has been completely obliterated on the left side, but on the right side we can still discern some trace of the overhang (Fraser, p. 260). The obliteration is due to the addition of bone below the mylohyoid line, as shown by the presence of some shelving away on the right side (max. transverse thickness of body = 20 mm.) and the left side (max. transverse thickness of body = 23 mm.). The left side has completely lost the normal shelving away. The alveolar bone has apparently remained unaltered on both sides of the jaw. The left sub-molar thickening has an irregular

lingual grooving partly overhung by a thin lamina of bone at one spot. This groove is apparently more or less continuous with the mylohyoid groove and extends forwards to within 1 cm. of the digastric fossa. About 6–8 definite minute foramina, presumably nutrient, are scattered around and along this groove, being possibly associated with the greater bulk of bone and its nutritive requirements. We have not observed them in normal mandibles. On the right side this grooving is absent, but the foramina are similarly distributed. When viewed from below both sub-molar thickenings are sharply defined anteromedially, possibly in correlation with the presence of the anterior belly of the digastric muscle (fig. 1). On the right side, the condition is more sharply defined, a definite smooth groove being present, extending back from the digastric fossa. There is a faint but definite grooving on the lower and

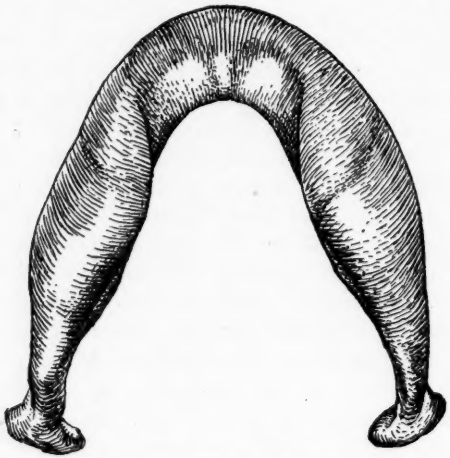

Fig. 1. Drawing of Mandible of Skull No. 856 from below. Not to scale.

outer sides of the right and left sub-molar thickenings. This groove lies anterior to the centre of the thickening and is more marked on the left side. At first we had thought this grooving was due to the external maxillary artery, but we came to the conclusion that it was probably too anterior in position and sloped forward too acutely, for it to be due to the artery. The thickening of the bone anteriorly has resulted in a "rounding off" of the chin, with disappearance of the mental tubercles. The greatest labio-lingual thickness of the bone here is on the left side of the chin region (22 mm.), this being in agreement with the greater thickness in the left molar region.

Anteriorly on the lingual aspect, the overgrowth of bone has been largely below the spina mentalis, but there has almost certainly been some overgrowth above the spine, inasmuch as we find the bone above the spina mentalis is raised into a broad transverse elevation, in contrast to the usual flat surface

to be seen here. This transverse ridge leads to the formation of what may be called a negative pit below it, the spina mentalis lying partly in and partly below this pit. Above, this ridge shades off into the alveolar bone, being itself 9–10 mm. in vertical extent. The digastric fossae are somewhat smooth and ill-defined. On the outer aspect of the body on both sides the linea obliqua presents a distinct projection, immediately below the third molar. This projection somewhat resembles a swelling frequently to be seen in what are apparently perfectly normal jaws. This swelling we have termed the trihedral eminence, when seen in the normal jaw.

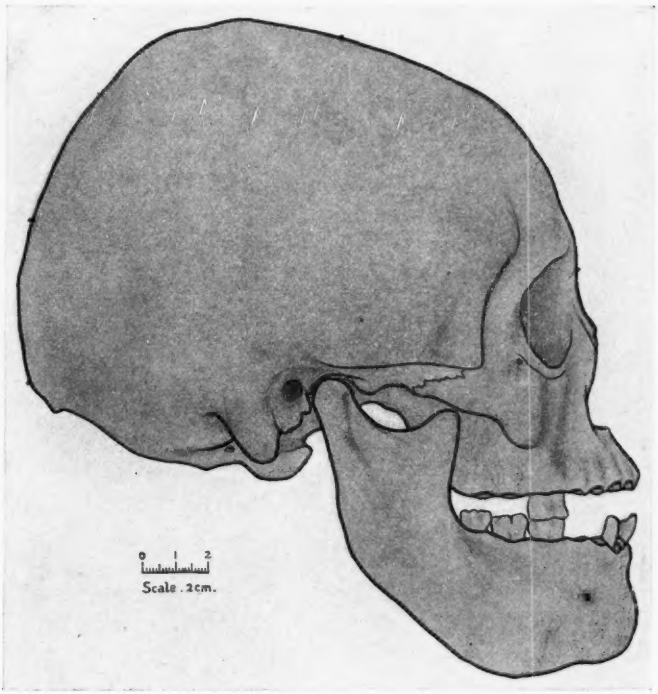

Fig. 2. Orthogonal projection of Norma Lateralis of Skull No. 856.

The mental foramen on the right side is below the alveolar ridge between Pm. 1 and 2. On the left side it is approximately below Pm. 2. Both foramina lie approximately at the normal level below the alveolar margin. The alveolus and the sockets will be considered when describing the teeth. The characteristic features of the rami are (1) their obliquity and the slight but definite elongation of the condyloid process (fig. 2), and (2) the poor development of the muscular markings (e.g. masseteric and internal pterygoid). As regards the degree of obliquity and elongation of the ramus, we believe that, while

by no means usual, it lies within the normal range of variation. The angle of the jaw on both sides has been greatly flattened out, and is consequently very difficult to define. This rounding off of the angle is partly due to the heaping up of the bone in the molar thickenings. Hence the mandible belongs to the form which, when seen in the normal jaw, is sometimes called "rocking" (Sullivan). Another factor concerned in the rounding off of the angle may be the apparent elongation of the ramus, similar to that which is said to occur in acromegaly (Keith). We may mention here, however, that Geddes distinctly

Fig. 2*a*. Photograph of Norma Lateralis of Skull No. 856.

states that it is the body and not the ramus of the mandible which had elongated in the remarkable and apparently typical case of acromegaly described by him. The crista endocondyloidea, the torus verticalis, and the crista endocoronoidea are all present and well defined. No trace is to be seen of the linea intermedia (or mylopharyngeal line, Lenhossek).

As regards the internal structure, an examination of a cut section and of X-ray photographs, shows clearly the original outline of the mandible (fig. 4). To this original outline as much as 13 mm. of bone have been superposed in

some regions. This original outline forms a thick inner table of compact bone (up to 6 mm. in thickness), buried in the bone, but visible by X-ray and on section. It is separated from the outer, or surface layer of compact bone, by cancellous bone, which, however, is extremely dense, with only minute interspaces. The outer, or surface table varies from 1 to 5 mm. in thickness, being thinnest on the medial aspect. The original or inner compact layer is

Fig. 3. Photograph of Norma Facialis of Skull No. 856.

apparently broken through by cancellous tissue on either side, close to where it joins up with the surface compact layer. The fact that the inner table of bone agrees very closely both in shape, orientation, and absolute dimensions with a normal jaw, is the main argument in support of its representing the original outline of the jaw. On attempting to correlate our X-ray findings with those given by Walkhoff, certain discrepancies were observed. The so-

called trajectorium dentale seems to show up very markedly, while the trajectorium basale seems to be narrower than normal as it approaches the head of the condyle.

THE INTERNAL ARCHITECTURE OF THE NORMAL MANDIBLE

Further study of X-ray photographs, and sections of aboriginal and other jaws, led us to the conclusion that the ramus of the jaw could best be considered as a tube extending obliquely from the condyle into the body of the bone. We found, however, that Walkhoff had already elaborated this view, although subsequent workers had not fully realised this, nor are Walkhoff's figures by any means clear upon the subject. The upper portion of this tube extends from the head of the mandible to the mandibular foramen. Its interior is filled with cancellous bone. In the mandible of the Australian aboriginal, the tube is often almost rounded on section, and projects sometimes more markedly on the outer side of the ramus, and sometimes more markedly on the inner side, having been termed the crista ectocoronoidea, and the crista endocoronoidea respectively. Even below the mandibular foramen, this tube-like structure may be discerned, with the mandibular canal in its interior (fig. 5). The walls of the mandibular canal are thick and well defined here, possibly in compensation for some weakening of the bone as a whole, both from perforation and loss of cancellous tissue. In cases of relatively slight development of the jaw (as in many European skulls), the tube becomes flattened from side to side, being oval in section, and is largely obscured, in contrast to the powerful mandibles of many Australian aboriginals, in which the tube more nearly approximates to a true cylinder. The tubular structure may also be obscured in powerfully developed European mandibles. In these cases, we incline to the belief that the ramus is more upright, and the mandible more orthognathous than in aboriginal jaws, thus obviating the mechanical necessity for marked development of the axial tube. We have not yet, however, confirmed this suggestion by accurate measurements and X-ray studies. Study of X-ray photographs of some specimens would seem to indicate that the bone tends to have a spiral arrangement in relation to the walls of this tubular axis though this could not be decided by study of sections of the bone. An examination of the jaw in old age seems to support the thesis that the essential structure of the ramus is a cylinder with coronoid and angular flanges. In one specimen examined by us (No. 860, A.D. Mus.), the ramus is reduced to an irregularly flanged bar or tube, extending from the condyle to the body, the

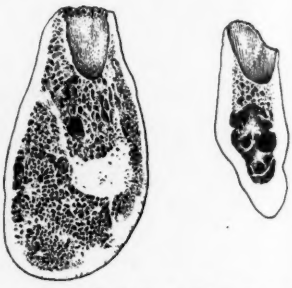

Fig. 4. Scale drawing of cut section of left half of Mandible of No. 856 compared with a similar section of a normal European mandible (both sections through the posterior root socket of the second molar tooth).

angle having been practically lost. In this particular specimen also, the trihedral eminence is well marked, indicating that its presence is not necessarily correlated with muscular development alone.

On examining X-ray photographs and casts of the Piltdown mandible (Underwood), we find an interesting condition. While the external features of the ramus are definitely anthropoid (Underwood, Lenhossek, etc.), the internal architecture shows a close approximation to that of a powerfully developed human jaw. When we examine X-ray photographs and specimens of adult mandibles of the Orangutan, Chimpanzee and Gorilla, we find that

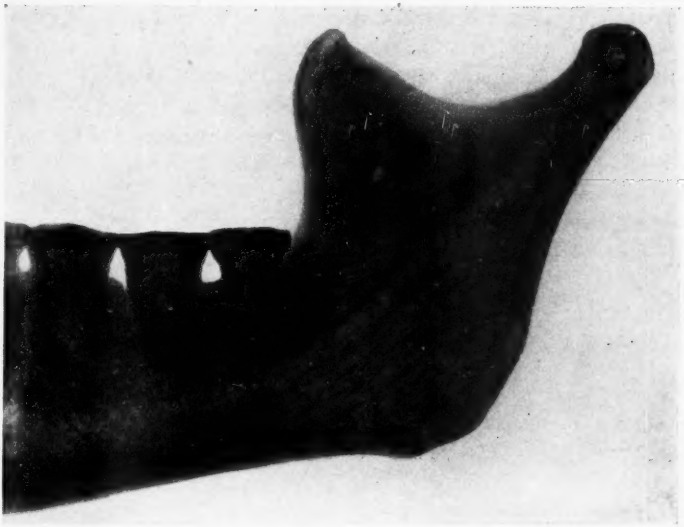

Fig. 5. X-ray photograph of Mandible of Australian aboriginal. Right side (No. 2356. Mus. N. and M. Anatomy).

the tube-like structure in these is lost, being overshadowed by the marked development of muscular trajectoria (see Walkhoff, Selenka, pp. 242 to 246). Of these trajectoria, the radiate ones are well marked. In the Piltdown mandible, however, we can see this tube-like appearance in the X-ray photograph, although the tube is somewhat broader than in any human specimens I have seen; the radiate trajectoria are absent in the Piltdown. Thus the Piltdown mandible approximates more closely to the human condition in the internal architecture of its ramus than in its external features.

THE TRIHEDRAL EMINENCE

We have already referred to a projection frequently seen in the normal jaw of all races, which we have termed the trihedral eminence. We have found it in a number of skulls (Nos. 815, 219*a*, 221, 838, 834, 832, Anatomy Dept.

Museum) of all races, Australian aboriginal, New Guinea, Solomon Islands, African negro, Egyptian, and European. We have called this projection provisionally the "trihedral eminence" of the mandible, because in those jaws which present this feature most markedly, it forms a distinct flat based, shallow pyramid, one side being a continuation of the outer border of the alveolus, the second being continuous with the ramus posteriorly, and the third with the body of the bone below and anteriorly. A striking example is shown in fig. 6. We believe that a well-marked eminence may possibly be correlated to some degree with mechanical factors. The presence or absence of the trihedral eminence is probably dependent to a great extent upon the angle of inclination of the plane of the ramus, to the plane of the body. The alveolus, the body, and the ramus each form an independent plane, the trihedral eminence being formed at their junction. The eminence would also seem

Fig. 6. Drawing of Mandible No. 219, A.D. (Solomon Islands) showing marked trihedral eminences.

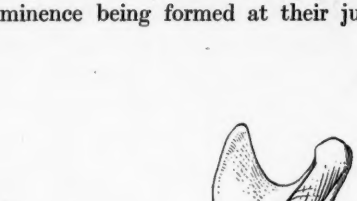

Fig. 7. Diagram suggesting the essential tubular axis of the ramus of the Mandible, and its relation to the trihedral eminence.

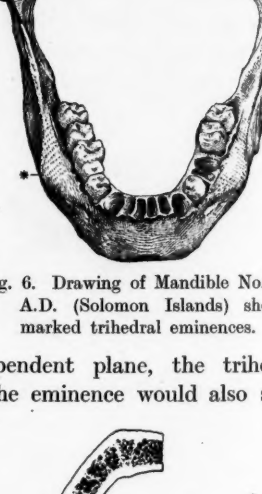

Fig. 8. *A*. Horizontal section of half a Mandible suggesting the girder-like structure of the ramus and body of the Mandible, the thickest portions of the girder being indicated by *, the larger of which is at the trihedral eminence. *B*. Vertical section of the body of the Mandible in the region of the second molar tooth, with arrows suggesting the forces correlated with the development of the trihedral eminence (indicated by *).

to be the point of greatest breadth in a girder-like structure into which the mandible can be dissected (fig. 8 *A*). This girder may be considered as running parallel to the lower border of the body into the ramus, the strongest

lateral point of the girder being at the trihedral eminence. It would be concerned in strengthening the mandible in lateral movements. Again, we have it as a meeting point for (*a*) pressure components from the teeth and (*b*) a tubular axis running through the ramus towards the trihedral eminence from the condyle (figs. 7 and 8*B*). Again, we may consider the molar teeth as being set upon the inner aspect of the body, the axis of their rests running downwards and outwards, to meet the tubular axis of the ramus, at an angle of 15°, when viewed from behind, forming an acute V. The apex of the V seems to be at or near the trihedral eminence, when it is present (fig 8*B*). It is doubtful whether the mandibular torus, seen in Icelandic, Eskimo, and other skulls (Hooton) can be compared with the trihedral eminence. It has been considered as forming a strengthening bracket on the inner side of the body of the mandible, more especially below the region of the molar teeth. That this is doubtful or only partly true is indicated by its almost complete absence in the mandible of the Australian aboriginal.

From the study of the internal architecture of the mandible, and of the trihedral eminence, the following working hypotheses emerge, and will probably prove of value in further studies. "That there are at least two relatively independent factors to be taken into consideration in studying the formation of the mandible, (1) the size and shape of the dental arches and (2) the degree of separation of the mandibular fossae on the base of the skull." Humphrey, writing in 1878 upon the growth of the mandible, said, "Though the bones of the alveolar arch are extended backwards, and the arch is rendered more elliptical, it is not widened. The widening of the jaw, in correspondence with the increasing width of the base of the skull, takes place almost entirely behind the alveolar arch in the ramus....Accordingly, we find that in infancy the rami of the jaw are in a line with the alveoli, whereas, subsequently, they diverge considerably, and a well-marked obtuse angle in a horizontal plane is formed, on either side, between the alveolar arch and the hinder portion of the jaw."

Stereoscopic radiography of the ramus and mandible will also probably give us further information as to the structure of the ramus and body of the mandible, while the study of the relationship of the coronoid process and the angle to the tubular axis, may throw some light on racial differences in the mandible, such differences being somewhat chaotic at present.

TEETH AND TEETH SOCKETS

In the few teeth that remain, the degree of wear is about the same as that usually found in New Guinea skulls. It corresponds to Broca's No. 1, no dentine being exposed except in two anterior teeth of the lower jaw. The teeth now present are, in the upper jaw, the first molars only; in the lower jaw, all the molars, except the first left molar, are present, and also the first right incisor, and the right canine tooth. To confirm the impression already mentioned that the sockets of all the teeth have been reduced in depth, we

have measured the depth of the sockets in both the mandible and maxilla in twelve carefully chosen, normal New Guinea skulls, besides confirming our statements by a general review of other skulls. These measurements would show that there is a marked general reduction of the depth of the sockets in No. 856. On graphing these results, and comparing also with the average socket depth in European skulls (deduced by deducting 3 mm. from the average root length), it was at once apparent that the anterior teeth have been affected to a greater degree than the cheek teeth, this being most marked in the mandible. Incidentally, our scanty figures would indicate that the tooth sockets in the New Guinea native are of greater depth than in the European. This, however, would require extensive investigation, and obviously, age, wear of teeth, etc. would all have to be carefully considered. We believe that there is no evidence of any local dental disease to be found in No. 856 (e.g. pyorrhea alveolaris, etc.). The alveolar borders show no signs of excavation, or deviation from the normal, and further corroboration is given by the fact that the roots of the teeth show no undue exposure from bony absorption at the neck, being perfectly normal in this respect. In the case of the molar teeth, there is some suggestion of "crowding" or bunching of the roots, inasmuch as the second lower molar teeth, on both sides, show complete fusion of the roots along one edge. The sockets of the second upper molars indicate a similar condition to have been present. The third lower molar teeth also have marked root crowding, with incomplete fusion, as is of course frequently the case normally. The sockets of the upper wisdom teeth indicate that their roots were probably fused.

The roots of the upper and lower first molars, on the other hand, are perfectly normal except for the reduction in the socket depth, thus possibly giving some indication of the age at which the abnormality commenced, i.e. at, or about, twelve years of age.

We have already mentioned the remarkable upgrowth of bone into the interior of the lower incisor and canine teeth, which led to their retention and preservation. The bone has grown from the buccal wall of the socket, entered the root canal and there expanded. The teeth thus retained are the first right incisor and the right canine. By chance the crown of the canine has been partly fractured, and the interior of the pulp cavity partly revealed. This fracture shows the pulp cavity and dentine to be normal macroscopically. On looking down the pulp cavity into the root canal, the bony pillar can be seen. Two other sockets, e.g. those for the left first incisor and the right, second incisor, show a similarly projecting ingrowth from the socket wall, but to a lesser degree, so that these teeth were lost in spite of it. The left canine socket shows very doubtful evidence of such an abnormality. In the upper jaw, there is no trace of any similar projection in any of the tooth sockets. We are unable to find any record of a parallel case. Scheff, in recording the rare cases of bony union between the alveolus and the root of a tooth, records only cases where the bone has fused apparently with the cement or dentine

on the exterior of the root, although one of his figures shows bone in the interior of a mass of dentine. It is probably impossible to determine whether the teeth in No. 856 were ever fused with this bony pillar. An X-ray photograph also confirms the presence of this bony pillar.

It is doubtful whether the lamina dura of the remaining mandibular tooth sockets shows any marked thickening, though there is some indication of this.

The teeth are microdont, with a dental index of 40·8 (Flower) and present no abnormalities in their crowns. The occlusion, so far as can be determined, was quite normal, as shown by the relations of the first molars, and the faceting of the remaining molars and the lower incisor and canine. The wear on these latter teeth would indicate a true edge to edge bite.

THE UPPER FACIAL SKELETON AND THE CALVARIUM

The cranium, if unaccompanied by the mandible, would not attract attention. Nevertheless, a careful examination reveals several features, which while not without the normal range of variation are still probably correlated with the changes seen in the lower jaw.

The tooth sockets of the maxilla are shallowed, to nearly the same extent as in the mandible. The outer alveolar wall in no case shows the perforation near the root apex, which is so frequently seen in weathered normal skulls. This lends some support to the independent observation that the bone is denser than normal.

Except for a slight torus palatinus, the palate presents no features of interest, and is not increased in area. The nasal aperture is normal, with a gutter-like lower margin (orygmocraspedote) and is mesorhinic (Hrdlicka).

The maxillae and zygomatic bones while powerful and well developed are normal. At the maxillo-jugal suture, on the lower orbital margin, the bone projects as a tubercle, while the lower and outer orbital margin is definitely thickened to form a definite beaded edge, with a sharply defined lower margin. This thickened margin results in the outer floor of the orbit forming a deep fossa, extending back to the inferior orbital fissure. The bony floor of this fossa is thickened so as to be opaque to light. The outer surface of the fronto-sphenoidal process of the zygomatic bone is definitely porous and corroded.

The roof of the orbits is hollowed to a similar, but lesser degree than the floor. The supraorbital and glabellar regions present no abnormal features, except that the supraorbital notch is converted into a foramen on the left side, the right side having the usual notch. This fact is of importance, when we remember that it is the left side of the mandible which shows the grossest change.

The skull is dolichocranial and beloid (Arrow head, Sergi), in form. The sutures vary from No. 3 to No. 4 of Broca's table and nowhere show obliteration. The coronal suture presents a peculiar depression, 25 mm. in length on either side, in the region of the temporal crest. The depression is accentuated by a coincident elevation of the temporal ridge behind and below it (fig. 3).

The foramen magnum is relatively rounded and has an index of 90 (see Keith, 1911).

The region of the pterygoid laminae and posterior nares gives an impression of elongation, but we hesitate to consider this more than a personal impression.

The bones of the cranial vault, from approximate measurements, are not more thickened than normal.

We would draw attention to the remarkably small cranial capacity, e.g. 1010 c.c. The pituitary fossa was not enlarged; further work is being carried out by one of us (J. E. G.) to determine its relationship to the racial dimensions in the Papuan.

The principal measurements of skull No. 156 A.D. (Sydney University) are: Cranial capacity, 1010 c.c.; maximum length 170 mm.; maximum breadth 122 mm.; cephalic index 71·8; basi-bregmatic height 120 mm.; vertical index 70·6; auriculo-bregmatic height 101 mm.; minimum frontal breadth 77 mm.; basion-nasion 98 mm.; basion-prosthion 104 mm.; gnathic index (Flower) 106·1; bizygomatic breadth 120 mm.; face height (nasion-gnathion) 115 mm.; nasion-prosthion 66 mm.; nasal height 50 mm.; nasal width 25 mm.; nasal index 50; orbital width 41 mm.; orbital height 31 mm.; inter-orbital width 20 mm.; maxillo-alveolar length 60 mm.; maxillo-alveolar breadth 65 mm.; foramen magnum length 31 mm.; foramen magnum width 28 mm.; naso-malar arc 107 mm.; naso-malar chord 99 mm.; mandible, symphyseal height 37 mm.; body height, right 41 mm., left 40 mm.; bigonial width 99 mm.; gonio-mental length 93 mm.; gonion to incisive point 91 mm.; taking the occlusal plane of the teeth and projecting the mandible upon this, the length from the most anterior point to the mid-point of the line joining the hinder borders of the condyles is 101 mm.; from this latter point to the line joining the tips of the coronoid processes is 43 mm. (Thomson, 1903).

The modulus of the skull is 137·3 and the weight without mandible, but including the two upper first molars, is 545 gm. This weight does not differ from the weights of normal skulls with approximately similar moduli. The weight of the mandible with the two anterior teeth only is 125 gm.

GENERAL DISCUSSION

The condition described does not seem to correspond exactly to any previously recorded case, so far as we are aware. We believe that the abnormality is not due to any known local disease of the teeth or jaws. The absence of any erosion of the alveolar bone and of caries of the teeth support this contention. The roots of the teeth show a normal degree of exposure. Further, the marked symmetry and relatively wide distribution of the bony change are unusual in local disease. On comparison with *acromegalic skulls* (Keith, Thomson and Geddes), it is clear that agreement is to be found only in a few features. The difficulty of comparison is increased by certain apparent contradictions in the description of acromegalic skulls by previous observers. Keith (1922) definitely states that the elongation of the mandible in acro-

megaly is due to subcondyloid growth of the ramus, whereas Geddes says that in some well-marked cases (E.A.S. 07 and three Irish giants), the elongation of the mandible apparently takes place chiefly in the body of the bone. In other cases quoted by Geddes, the measurements show that there must have been considerable elongation of the ramus. Our specimen shows a little elongation, but there has been no interference with occlusion. The thickening of the body is different from that usually seen in acromegaly, although this may possibly have some correlation with the fact that the molar teeth are almost completely absent in the specimens figured by Keith and Geddes. The slight but definite osteoporosis present on the left molar bone may have some significance. Geddes' case showed extensive osteoporosis in the upper facial skeleton. The condition differs from acromegaly in the limitation of the bone overgrowth largely to the mandible. The pituitary fossa, also, is not enlarged. The upper facial height and the total facial height do not show any marked increase when compared with the normal Papuan skull of a similar type. The orbital outline is normal and the superior maxillae are not increased in alveolo-orbital depth. It is thus clear that the condition does not resemble the advanced stage of acromegaly.

So far as we can determine, there is little but a superficial resemblance to the rare condition called *leontiasis ossea*. This condition is said to commence usually in the upper facial bones and terminates in a condition which has been variously described. Choyce states that hard compact bone is present. Morton quotes Erichsen as saying in the 10th edition of his *Surgery*, 1895, "The new bone is spongy in structure, and in the few recorded cases the disease has begun early in life." X-ray figures of Morton's case, however, show that the disease had involved the lower jaw to a marked degree, even more so than in our specimen, and also that the bone was apparently very dense, or at least, if porous, it was so thick as to throw a dense shadow. Telford, in a review of the literature in 1914, states that the enlargement of bone begins in the orbital region, the most marked changes being usually seen in the upper jaw, whilst the lower jaw is quite often unaffected; the surface of the bones is, as a rule, smooth, but may be markedly irregular from the presence of nodular osteomatous outgrowths. The bone may show dense ivory induration, or may, on the other hand, be easily pared with a knife, as in a case mentioned by Keen. The distinction of the inner and outer tables and diploe is largely lost. This was not the case in No. 856.

It is probable that the great variability in the bony structure which is found in these various generalised bone diseases, is due not only to the intensity and time period of the diseased process, but also to the variability of normal factors, e.g. function, which is often affected by the hypertrophy, etc.

As regards Paget's disease, or *osteitis deformans*, the skull exhibits scarcely any correspondence with specimens available to us, or with current descriptions. The lower jaw, from a complete skeleton of a case of osteitis deformans examined by us (Mus. Normal and Morbid Anatomy, Sydney University

Medical School), shows marked overgrowth, but only in correspondence with the rest of the cranium, and moreover the alveolus shares in this overgrowth, and the texture of the bone was much more porous.

Unilateral hypertrophy of the skull, and the skull condition found in dystocia adiposo-genitalis may be dismissed.

The condition, so far as we are aware, presents none of the usual features of syphilitic disease of the bone, nor of framboesia, while actinomycosis, rickets, tubercle, and odontomata can be excluded. The condition known as "boomerang leg," a symmetrical disease of the tibiae seen especially in aboriginals of Northern Australia and of New Guinea, presents some analogies. The X-ray photographs and the macroscopic appearance of bone sections resemble those seen in the mandible of No. 856. Breinl and Priestley suggest that the boomerang tibia is due to a chronic osteomyelitis (? cause), and state that the first stage is in the form of a rarefying osteitis, later followed by a condensing osteitis. It is thus possible that some tropical disease may ultimately prove responsible for both conditions. If, however, it should be due to some endocrine disturbance, such as an early acromegaly, it would be of interest to find such a condition in a somewhat primitive race.

In attempting to explain why the mandible has been most affected, Keith's statement that the mandible is the most plastic bone in the body must be borne in mind. If then we suppose an endocrine disturbance as the initial cause, the condition would possibly first develop in the mandible if Keith's statement be true.

SUMMARY

The skull cannot be placed in any known category, as far as we are aware, and presents the following outstanding features; symmetrical enlargement of the body of the lower jaw, excepting the alveolus, a definite shallowing of the teeth sockets in both upper and lower jaws, and an upgrowth of bone into the pulp cavities of certain of the teeth. Of these features, the growth of bone into the pulp cavities of the anterior mandibular teeth, is, we believe, quite unique, and has not hitherto been observed.

NOTE. Since this was written, Mr J. Thornton Carter has kindly shown me a hitherto undescribed ground section of a tooth with bone irregularly invading the dentine of the root.

The cancellous bone in the interior of the body of the mandible is of a much denser character than normal, more especially that which has been superadded.

As regards the structure of the normal mandible, we would draw attention to the presence of the *trihedral eminence*, quite frequently to be seen in normal jaws of all races. The chief interest of this bony swelling lies in the added light it throws on the structure of the mandible, forming a further link in our knowledge of bone morphology. Further, we would again emphasise the essential tubular structure of the ramus of the mandible, as first elaborated

by Walkhoff. This tubular structure may be overshadowed by the extreme development of the muscular flanges, as in the jaw of the adult anthropoid ape, or on the other hand it may be reduced as in the lower jaw of many modern Europeans. In a powerfully developed human jaw bone (e.g. Australian aboriginal), the tubular structure is much more defined and obvious, the tube, on section, being rounded and not so flattened or oval as in the European. It is significant, then, that in the Piltdown jaw, while the external features of the ramus are definitely anthropoid (Smith Woodward, Underwood, etc.), the internal architecture shows some approximation to that of a powerfully developed human jaw. It is possible that these changes are largely a function of the absolute size of the jaw and teeth.

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THE EARLY STAGES OF THE DEVELOPMENT OF THE ILEO-COLIC SPHINCTER

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A perusal of the text-books of anatomy on the ileo-colic region of the gut shows that there is a divergence of opinion on the manner of action of the ileo-colic valve. There are, it is evident, two views. In the first, it is considered that at the junction of the small and large intestines the arrangements constitute a mechanical device, acting locally and automatically, to prevent regurgitation of the contents of the colon into the ileum. Some who uphold this view consider that the Valvula Coli acts much in the same way as the mitral valve of the heart, its two flaps being pressed together by the contents of the colon, and pulled together by the stretching of the frenula as the colon is filled (Birmingham, Cunningham); others regard the valve action to be due more to the obliquity of the entrance of the terminal ileum into the colon, in a manner analogous to the valve action of the intra-mural part of the ureter (Symington[1], Waterson[2]). The second view, advanced chiefly by Keith[3], regards the ileo-colic junction as a sphincteric mechanism which controls the exit of the ileal content and depends for its efficiency on a sphincter muscle surrounding the opening. Rutherford[4] has brought forward a series of observations on the histological structure of the junction in the human adult which supports this view and Elliott[5] has worked out the innervation of the sphincteric band in the cat, which also confirms it. There may also be said to be a third view, a combination of the first and second. In it, it is held that while a sphincter muscle is present, the efficiency of the junction is enhanced by the arrangement of its parts (Robinson, Howden). This view is, in all probability, the correct one, at least so far as human anatomy is concerned; but in order to determine the morphological value of the sphincter muscle it is necessary that the early stages of its development should be studied.

The observations on which the findings of this paper are based were made on a series of human embryos of the following lengths, for the loan of some of which I am indebted to Prof. T. H. Bryce, F.R.S.:—8 mms., 9·5 mms., 14·5 mms., 16·1 mms., 19 mms., 21 mms., 22 mms., 32 mms., and 40 mms.

At the 8 mm. and 9·5 mm. stages the mesoblastic covering of the gut in the ileo-colic region consists of a mass of undifferentiated cells, closely packed

[1] Quain's *Anatomy*, 11th ed.
[2] Cunningham's *Anatomy*, 4th ed.
[3] *Journ. Anat. and Phys.* 1903.
[4] "The Ileo-caecal valve," 1914.
[5] *Journ. Phys.* vol. xxxi, 1904.

together and rapidly proliferating. At the 14·5 mm. stage two layers can be defined in the mesoblast: (*a*) the serous coat which throughout the series remains as a layer one cell thick, the cells being cubical in the early stages and more flattened in the later, and (*b*) a middle[1] layer of the gut wall which will differentiate to form the submucous, the muscular, and the subserous coats.

At the 16·1 mm. stage it is possible to identify in the ileo-colic area the layer of cells from which will be developed the circular muscle coat of the gut. This layer differentiates from both the cranial and caudal ends of the gut tube, but the definition takes place at an earlier period and at a more rapid rate from the cranial end; and it is at this stage of development and from the cranial end that the process reaches the ileo-colic junction. At 19 mms. the myoblasts of this region have taken on the characteristic shape of embryonic muscle cells and are becoming well differentiated from the other cells of the mesenchymal coat of the bowel. After the 20 mm. stage it is possible to recognise at the ileo-colic junction a definite thickening of the

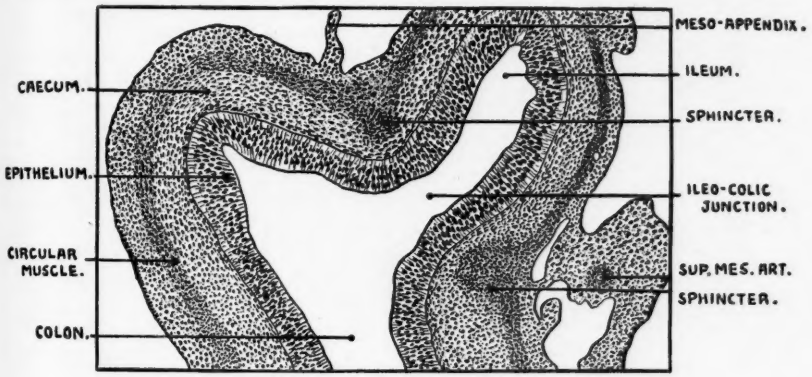

Fig. 1. The ileo-colic junction in a 40 mm. human embryo. (×150)

circular muscle layer. In embryos which have been sectioned horizontally the ileo-colic junction presents a Y-shaped appearance (fig. 1). The small limb on the left side of the Y represents the base of the caeco-appendicular anlage. The right limb represents the terminal ileum while the "leg" of the Y is the proximal colon. The angle between the small limbs can be called the ileo-caecal angle while the angle between the right limb and the "leg" of the Y can be called the ileo-colic angle (fig. 1). At the 21 mm. stage the myoblast layer becomes very much thickened in the region of the ileo-caecal angle, and forms almost one-half of the total thickness of the mesenchymal coat of the gut. The myoblast layer at the ileo-colic angle also becomes thickened but not to the same amount as at the ileo-caecal angle. In reconstructions this thickening of the circular muscle coat can be traced round the gut at the line

[1] The three layers of the gut wall at this stage are:—(*a*) the outer serous layer, (*b*) the middle mesoblastic layer, and (*c*) the inner endodermic epithelial layer.

of the junction of the ileum and the colon. The ileo-colic angle at this stage is about 140°.

After the 20 mm. stage the gut tube at the ileo-colic junction rapidly increases in diameter and the circular muscle coat becomes reduced in relative thickness in the terminal ileum and proximal colon; but the thickening of the circular muscle sphincter at the junction maintains its relative size. In the 32 mm. stage the ileo-colic angle has become a right angle, the terminal ileum now entering the colon from above and on the right. There is now at the junction (fig. 2) a well marked ring of muscle tissue which has invaded the sub-mucous layer of the gut and reduced it at the junction to a thin layer of cells; the outer or sub-serous layer remains of the same thickness as in the terminal ileum and proximal colon. [The sub-mucous layer develops later into the muscularis mucosae and the sub-mucous coat of adult anatomy and

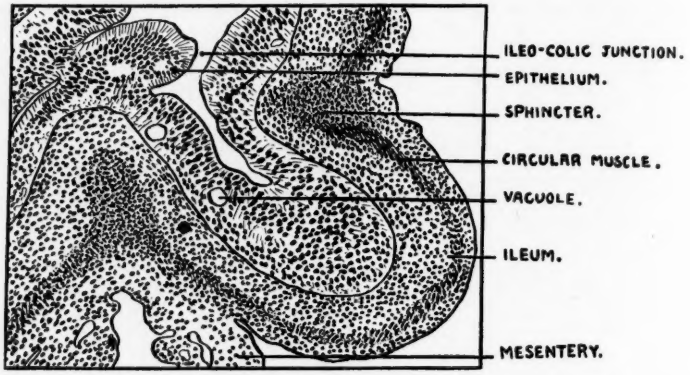

Fig. 2. The ileo-colic junction in a 32 mm. human embryo. (×200)

the sub-serous layer differentiates into the sub-serous coat and the longitudinal muscle layer; but at this stage in the ileo-colic region these differentiation processes have not commenced. The epithelial layer has proliferated rapidly and at this stage is becoming thrown into the ridges described by Johnston[1].] In the 40 mm. embryo (fig. 1) practically the same stages of development are seen, but there is a great increase in the size of the gut. The anlage of the sphincter is quite sharply marked off from the remainder of the gut wall and evidently it is growing at the same rate as the gut itself.

SUMMARY

1. The first coat of the adult intestine to differentiate is the serous coat. After this the circular muscle coat becomes differentiated in the "middle" layer of the mesenchymal coat of the gut wall.

[1] *Amer. Journ. of Anat.* vol. XIV.

2. The myoblasts can be recognised in the mesenchyme at the ileo-colic junction at the 14·5 mm. stage. They form a definite layer at the 19 mm. stage and from then onwards they form a thickening which can be recognised without difficulty.

3. As the ileo-colic angle diminishes and the gut wall further differentiates, between the 20 and 32 mm. stages, the anlage of the sphincter muscle becomes more defined and ring-like.

4. The early presence of the sphincter anlage, even while the ileo-colic angle is greater than a right angle, would seem to show that the sphincter is the essential element in the Valvula Coli and that the later arrangements in the terminal ileum and proximal colon are secondary in nature.

OBSERVATIONS ON THE ANATOMY OF THE HEART OF *TILIQUA SCINCOIDES* AND *EUNECTES MURINUS*[1]

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Prof. E. S. Goodrich in his paper "On the Classification of Reptilia" laid especial stress on the relation of the interventricular septum to the openings of the pulmonary and the right and left systemic arches, and concluded that "the Amniota diverged into two branches, the Sauropsidan branch culminating in Aves, the Therapsidan branch in the Mammalia." Dr Chas O'Donoghue, who investigated the structure of the hearts of Reptilia, while agreeing with the final conclusion of Prof. Goodrich "that no modern reptilian heart can lead to the Mammalian structure," is opposed to the statement of the latter author—"in the reptilia the interventricular septum tends to divide the chamber into a left cavity leading to the base of the right systemic arch and a right cavity leading to the base not only of the pulmonary but also of the left systemic arch," and is of the opinion that the statement is "incomplete and somewhat misleading" in regard to Lacertilia and Ophidia, and holds that "the conditions in Ophidia and Lacertilia are quite different from what is implied by Goodrich in the extract given above and in his diagram. The ventricle in these two groups containing by far the greatest number of living species is indeed partially divided into a right and left chamber but the two systemic arches come off from the right side and the pulmonary arch comes off from the left. There is thus a considerable difference in the relation of the septum to the arterial trunks between Ophidia and Lacertilia on the one hand and Crocodilia and Chelonia on the other.....In Ophidia and Lacertilia it lies between the pulmonary and systemic while in Crocodilia and Chelonia it lies between the pulmonary and the right systemico-carotid." Further "Another striking and important difference which has not been emphasized formerly is that whereas in the Crocodilia and Chelonia as in birds and mammals the aerated blood is poured into the left side of the ventricle, in Ophidia and Lacertilia the reverse is the case and the aerated blood passes into the right ventricular chamber." Prof. Goodrich in a later paper following the criticism of Dr O'Donoghue not only maintains his main findings but offers a critical review of O'Donoghue's contribution on the subject; he questioned, while correcting his own mistakes, the accuracy of the statement of O'Donoghue in regard to the course of blood in the Lacertilian and Ophidian hearts. The

[1] "Approved as Thesis for the Degree of Master of Science in the University of London."

discussion between Prof. Goodrich and Dr O'Donoghue regarding the exact position of the incomplete interventricular septum in the Reptilia and the relation of the septum to the origin of the pulmonary, left systemic and right systemico-carotid artery shows that in certain respects both the authors are agreed while in others they are at variance. Prof. Goodrich and Dr O'Donoghue have arrived at their conclusions from an examination of dissections and serial sections of the heart; it is clear from Goodrich's remarks that O'Donoghue has misinterpreted some of his observations and has consequently been led to untenable conclusions. It has been considered desirable to check the results of both these authors. Accordingly, at the suggestion of Prof. J. P. Hill, F.R.S., the investigation of the structure of the heart of the lizard, *Tiliqua Scincoides*, was undertaken. I am deeply indebted to Profs. J. P. Hill, F.R.S., and D. M. S. Watson, F.R.S., for criticism and advice throughout the course of this work. I am obliged to Mr T. L. Poulton of the Department of Anatomy for help with the figures.

For purposes of accurate study a wax model of the heart was reconstructed from serial sections of 20 μ thick, with a magnification of 25 diameters.

GENERAL DESCRIPTION

The heart of *Tiliqua Scincoides* is typically Lacertilian (fig. 1). It lies far back in the body and is enclosed in a closed serous bag, the pericardium, which encloses not only the heart proper but also the roots of the conus arteriosus. In shape the heart is conical, broad at the base, and tapers gradually to a rounded cone. The pericardium is firmly fixed to the left part of the ventricle and projects posteriorly as a mass of tissue, the gubernaculum cordis. This is present in reptiles but is not found in Aves or in Mammalia. In the spirit specimen after removal of the pericardium a few of the vessels of the wall of the heart could be made out with the aid of a hand lens.

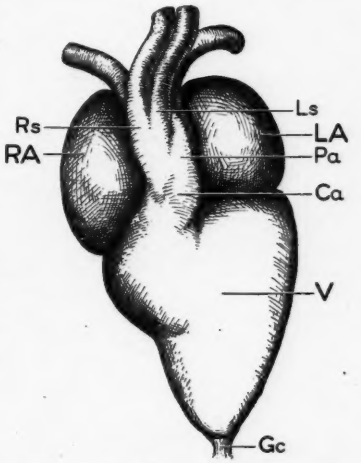


Fig. 1. Drawing of the heart (Ventral view). *C.a.* conus arteriosus; *G.c.* Gubernaculum cordis; *L.A.* Left auricle; *L.s.* Left systemic; *P.a.* Pulmonary artery; *R.A.* Right auricle; *R.s.* Right systemic; *V.* Ventricle.

The heart of *Tiliqua Scincoides* consists of the following parts (fig. 1):—

1. The Sinus Venosus.
2. The Right Auricle (fig. 1, *R.A.*).
3. The Left Auricle (*L.A.*).
4. The Ventricle (*V.*).
5. The Conus Arteriosus (*C.a.*).

1. *The Sinus Venosus.* The sinus venosus, although homologous with that of Pisces and Amphibia, is not clearly marked off externally as in either of

the two groups. It is closely attached to the right auricle, a little to the left, and it receives the anterior precaval veins and the post caval vein. The sinus walls are thin and do not call for any special remark. It may however be stated that neuro-muscular tissue occurs in the region of sinu-auricular valves. The sinus venosus leads directly to the right auricle. The sinu-auricular passage is a narrow slit at right angles to the long axis of the heart; it is guarded by a pair of well developed sinu-auricular valves. These valves lie cranially ($S.v._1$) and caudally ($S.v._2$) of the aperture; they are attached to the dorsal wall of the right auricle and project into its cavity. The caudal valve is larger than the other and overlaps it, but they are completely separated from each other (fig. 2, $S.v._1$, $S.v._2$).

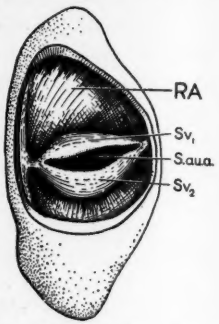


Fig. 2. The Right auricle of *Varanus niloticus*, cut open. *R.a.* The cavity of the Right auricle; $S.V._1$ and $S.V._2$ Semi-lunar valves guarding the *S.au.a.* sinu-auricular aperture.

The Auricles. The Right Auricle (*R.A.*). The right auricle of the reptile differs from that of birds and mammals. It is a large chamber with a comparatively thin wall. The walls of the auricle are provided, on the inner aspect, with muscular strands which are comparable with the pectinate muscles of the hearts of higher vertebrates. The entire cavity is lined by endothelium. The outer surface of the auricle presents some protuberances which correspond to the disposition of the muscle strands in the interior. The right auricle is completely separated from the left auricle by a well developed inter-auricular septum. The auricle leads into the ventricle by a narrow opening which is guarded by a large flaplike membranous valve (*A.v.v.*). The valve is attached to the lower end of the interauricular septum. The interauricular septum is not quite vertically disposed but is oblique and has its concave surface towards the cavity of the right auricle. It is not quite tensely stretched.

The Left Auricle (*L.A.*). The left auricle is much smaller than the right and receives only the pulmonary vein. The opening of the pulmonary vein is not guarded by any valves. The auricle leads by a very narrow opening into the ventricle. The auriculo-ventricular aperture is guarded by a membranous valve attached to the lower end of the interauricular septum. The auriculo-ventricular passage is elongated in an antero-posterior direction and is oval in cross section.

The Auriculo-Ventricular Valve (*A.v.v.*). Each auriculo-ventricular opening is guarded by a single valve; when viewed from the ventricle these valves have a common bell-shaped surface and can only be distinguished from one another by their dorsal and ventral attachments to the walls of the ventricle. The interauricular septum ends by becoming continuous with the anterior surface of these joint valves. The valve is not muscular but at the junction of the interauricular septum and the valve there appears to be a small amount of muscular tissue.

The Ventricle. The structure of the ventricle is indeed very remarkable. The wall of the ventricle is very strongly built. The cavity of the ventricle is divided by a number of muscular trabeculae, of varied development, into a number of confluent chambers. The ventricle is therefore incompletely divided, and three cavities communicating with each other may easily be recognized in it. There is in the first instance a muscular ridge (fig. 3*a* ***R.***) springing from the posterior apical wall which divides the ventricular cavity into a left and right cavity. The left cavity (***L.V.*** fig. 3*a*) may be said to be the *incipient left ventricle because the left auricle leads into it and the current of aerated blood falls into it.*

The right cavity presents some remarkable features. There is very posteriorly and ventrally a chamber (fig. 3*a*, ***C.P.***) from which the *pulmonary*

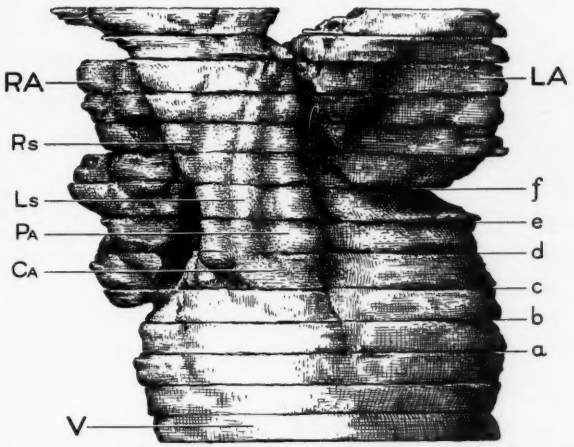


Fig. 3. Drawing of part of the wax model of the heart of *Tiliqua Scincoides* (Ventral view). *C.a.* conus arteriosus; *L.a.* Left auricle; *L.s.* Left systemic artery; *P.a.* Pulmonary artery; *R.a.* Right auricle; *R.s.* Right systemic artery; *V.* ventricle; *a, b, c, d, e, f,* are the levels, drawings of sections through which are shown in figures 3*a*, 3*b*, 3*c*, 3*d*, 3*e*, and 3*f*.

artery springs. This chamber is at once recognized as the "cavum pulmonale" of Goodrich and other authors. This comparatively small cavity communicates with a larger cavity by a very narrow passage. This large part of the ventricle receives the venous blood from the right auricle. This cavity is therefore the *cavum venosum.* The cavum venosum is separated to some extent from the cavum pulmonale by a thick muscular septum. The septum is continuous with the ventral wall of the ventricular chamber and extends in a dorsal direction towards the right in an oblique plane which on the whole presents part of a very graceful curve. This septum is the real interventricular septum, and should on no account be confused with other muscular projections into the cavity of the ventricle. This muscular septum has a very broad ventral base and a blunt rounded apex which is free (fig. 3*b*, ***V.S.***).

The Cavum Pulmonale. The pulmonary artery arises from the ventro-lateral chamber (cavum pulmonale), i.e. from the cavity to the right of the interventricular septum. The artery is very wide and the opening into the vessel is guarded by two semi-lunar valves (fig. 3*a*, 3*b*, ***P.S.V.***), which are laterally placed. The left semi-lunar valve is much larger than the right semi-lunar valve, and when the closure of the valve is effected the passage

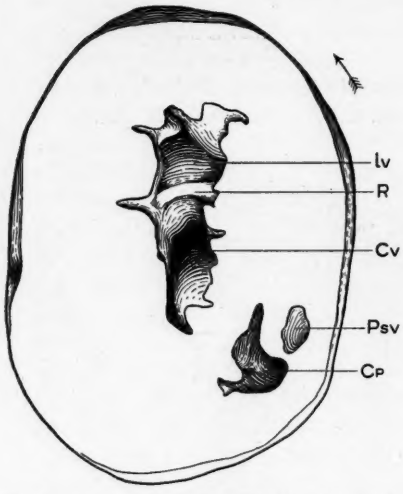


Fig. 3*a*. Drawing to illustrate the structure of the ventricle. *C.p.* Cavum pulmoneum; *C.v.* Cavum venosum; *L.v.* Incipient left ventricle; *R.* Ridge separating the cavum venosum and the incipient left ventricle; *P.s.v.* Semi-lunar valve guarding the pulmonary artery.

Note: cavum pulmoneum is completely separated from cavum venosum.

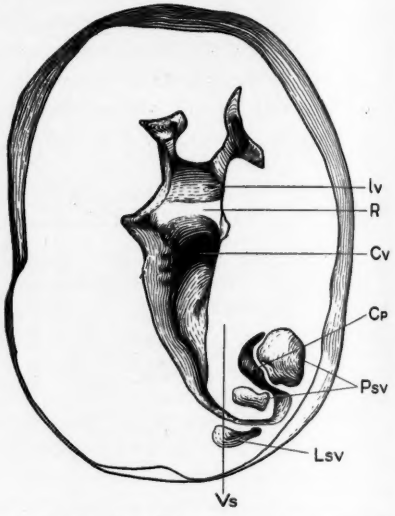


Fig. 3*b*. Drawing of the wax model of the ventricle to show the structure cranial to 3*a*. The cavum venosum and cavum pulmoneum are continuous at this level. Cavum venosum (*C.v.*) is larger in dimension. The left systemic has just appeared. *C.p.* Cavum pulmoneum; *P.s.v.* Semi-lunar valves at the beginning of pulmonary artery; the left valve is larger than the right; *L.s.v.* Semi-lunar valve of the left systemic artery; *R.* Ridge separating cavum venosum and cavum pulmoneum; *L.v.* Incipient left ventricle; *V.s.* Well developed interventricular incomplete septum.

Note: It is ventral in position.

to the pulmonary artery is obliterated. The cavum pulmonale is continuous, as already stated, round the free margin of the interventricular septum with the cavum venosum. Just at this level where the two cavities become continuous, there is, to the extreme right in the passage, the opening leading to the left systemic arch. The opening is guarded by two comparatively small semi-lunar valves (fig. 3*b*, 3*c*, ***L.s.v.***). These valves may be spoken of as the right and left valves. It is necessary to draw attention to the small size of

the aperture leading to the left systemic arch and its relatively anterior position.

The Cavum Venosum. From the cavum venosum springs a very large right systemo-carotid artery. The aperture leading to this important artery is situated even more anteriorly than that of the left systemic arch. The aperture is also guarded by two large semi-lunar valves (fig. 3*c*, 3*d*, ***R.S.V.***). The relative positions of the apertures of the pulmonary, left systemic and right systemo-carotid arches has escaped the attention of Prof. Goodrich and

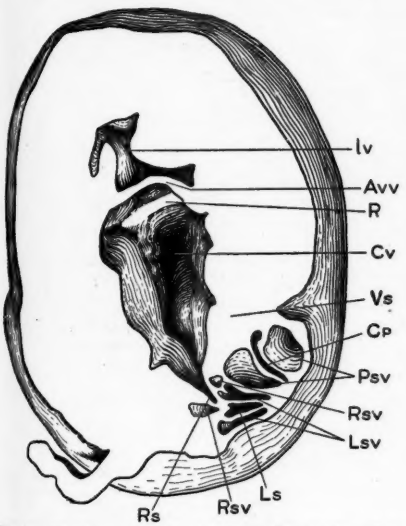


Fig. 3*c*. Drawing of the model cranial to 3*b*. *C.p.* Cavum pulmoneum with *P.s.v.* semi-lunar valves; *L.s.* Left systemic artery with *L.s.v.* Semi-lunar valves; *R.s.* Right systemic artery with *R.s.v.* Semi-lunar valves; *R.* Ridge separating incipient left ventricle and cavum venosum; *A.v.v.* The lower cut end of the left auriculo-ventricular valve; *V.s.* Ventral interventricular septum; *L.v.* Incipient left ventricle; *C.v.* Cavum venosum.

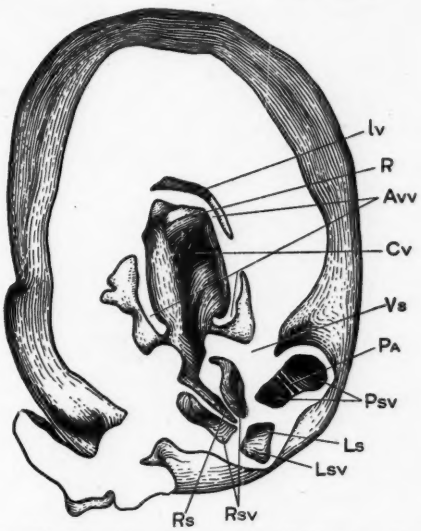


Fig. 3*d*. Drawing of the model. Section passing through cranially to 3*c*. *P.a.* Pulmonary artery with *P.s.v.* Semi-lunar valves; *R.s.* Right systemic artery with *R.s.v.* Semi-lunar valves at its commencement; *L.s.* Left systemic artery and semi-lunar valves (*L.s.v.*); *V.s.* Ventral interventricular septum; *L.v.* Left ventricle (incipient); *R.* Ridge; *C.v.* Cavum venosum; *A.v.v.* Cut ends of auriculo-ventricular valves.

Dr O'Donoghue. Devaz (6) does not make any reference to the positions of these apertures in his Thesis on the heart. Parker and Haswell in their *Text Book of Zoology* refer only to the relation of the interventricular septum to the three arches. The importance of the study of the exact position of these apertures will become apparent when the blood supply to the three arches is considered.

The ventral septum shows in addition some very interesting histological detail for a Lacertilian heart. It contains a rod of cartilage. The length of the cartilaginous piece is approximately 580 μ and it is more or less cylindrical.

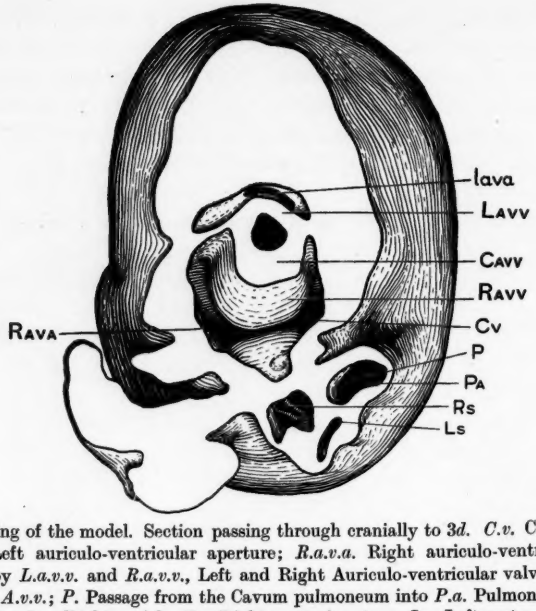


Fig. 3*e*. Drawing of the model. Section passing through cranially to 3*d*. *C.v.* Cavum venosum. *L.a.v.a.* Left auriculo-ventricular aperture; *R.a.v.a.* Right auriculo-ventricular aperture guarded by *L.a.v.v.* and *R.a.v.v.*, Left and Right Auriculo-ventricular valves; *C.a.v.v.* Cut surface of *A.v.v.*; *P.* Passage from the Cavum pulmoneum into *P.a.* Pulmonary artery; *L.a.* Left auricle; *R.a.* Right auricle; *R.s.* Right systemic artery; *L.s.* Left systemic artery.

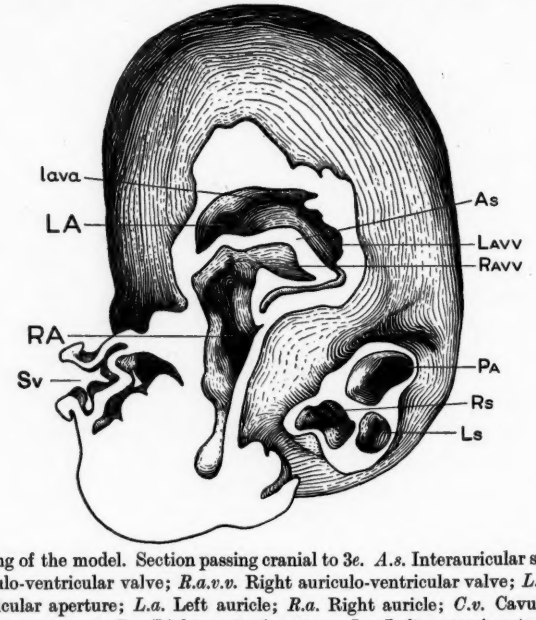


Fig. 3*f*. Drawing of the model. Section passing cranial to 3*e*. *A.s.* Interauricular septum; *L.a.v.v.* Left auriculo-ventricular valve; *R.a.v.v.* Right auriculo-ventricular valve; *L.a.v.a.* Left auriculo-ventricular aperture; *L.a.* Left auricle; *R.a.* Right auricle; *C.v.* Cavum pulmoneum; *P.a.* Pulmonary artery; *R.s.* Right systemic artery; *L.s.* Left systemic artery. In this part of the sinus venosus (*S.v.*) is just appearing.

The cells have not stained deeply though the nuclei stand out very prominently. This cartilaginous structure in the ventricular septum of Lacertilian hearts has escaped the attention of Prof. Goodrich and Dr O'Donoghue. It is rather difficult to specify the nature of the cartilage. The cells are large, polygonal, sometimes rounded, and have pronounced nuclei. It may be correct to describe the cartilage as parenchymatous in nature, although sometimes it simulates hyaline cartilage.

The Conus Arteriosus. The term "conus arteriosus" cannot be applied very rigidly to denote the apparently single vessel that arises from the ventricle. The term strictly speaking should be restricted to the basal part of the "conus arteriosus." I have observed in Testudo that the basal part of the conus arteriosus exhibits a rhythmical contraction showing that it really is part of the heart. The three arteries, the pulmonary artery, the left systemic artery, and the right systemo-carotid artery, are all bound together and enclosed by a common external covering. A spiral arrangement of the vessels leads to the pulmonary artery, which is originally situated on the left side ventrally, gradually shifting the position till at last it becomes dorsal. It soon branches into two, one to each of the lungs. The left systemic artery changes its position a little, and the right systemo-carotid artery gives rise to the subclavian and carotid arteries.

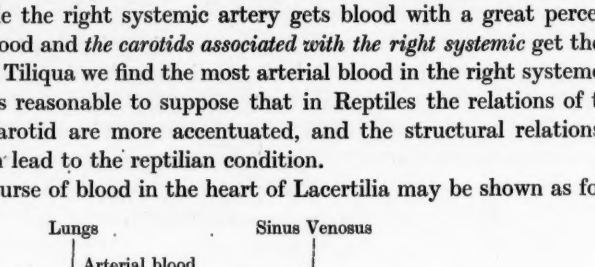
Two very beautiful dissections of the heart of *Varanus niloticus* by Dr A. Girgis were available for examination and study of the interventricular septum and the origin of the arteries specially. The relative positions of the ventricular chambers in the Lacertilian is the same as in Tiliqua.

Blood Supply to the three Arches. The supply of blood to the three arches remains to be considered. The right auricle receives as is known the venous blood from the sinus venosus, and the left auricle receives oxygenated blood from the lungs through the pulmonary veins. The two auricles contract at the same time. During the auricular systole blood from the right and left auricles flows into the cavum venosum and the cavum aorticum (the incipient left ventricle). Further during the auricular systole the cavum pulmonale becomes filled with venous blood which flows over the free curved border of the interventricular septum. When, after the end of the auricular systole, the ventricle begins to contract, this blood is forced onward and is replaced by more blood coming from the cavum venosum. This blood is forced directly into the *pulmonary arch*, whose lumen is very wide, in which the pressure is small and whose opening is the most caudal. The cavum venosum is partly emptied and as the ventricle continues to contract part of the blood from the cavum aorticum flows across the ridge into the cavum venosum and mixes with the venous blood in it. This left mixed blood is forced into the left systemic arch, the opening of which is relatively anteriorly situated and which has a pair of small valves, by the contraction of the ventricle. It should be noticed that it is the mixed blood that enters the left systemic arch. As the contraction proceeds, the remaining blood in the incipient left ventricle flows

across the ridge, and finding the pressure in the left systemic arch great flows into the most anteriorly situated but comparatively wide right systemo-carotid trunk. Thus then it is seen that most arterial blood is supplied to the right systemo-carotid arch in Tiliqua.

It may be interesting to observe that in the Anura most of the venous blood goes into the pulmo-cutaneous arch, and mixed blood to the left systemic arch, while the right systemic artery gets blood with a great percentage of arterial blood and *the carotids associated with the right systemic* get the arterial blood. In Tiliqua we find the most arterial blood in the right systemo-carotid arch. It is reasonable to suppose that in Reptiles the relations of the right systemo-carotid are more accentuated, and the structural relations of the amphibian lead to the reptilian condition.

The course of blood in the heart of Lacertilia may be shown as follows:—



Eunectes Murinus (The Anaconda). A large heart of a female eunectes from the collection of Prof. J. P. Hill was examined to study its gross structure in general and the relations of the interventricular septum to the opening of the arterial arches in particular.

The large heart is enclosed by the pericardial membrane. The heart is typically Ophidian in character and consists of the following parts:—

(*a*) The Sinus Venosus.
(*b*) The Right and Left Auricles.
(*c*) The Ventricle.
(*d*) The Conus Arteriosus.

The Sinus Venosus. The sinus venosus is a large cavity with thin walls situated on the dorsal aspect of the right auricle, and, though morphologically comparable with that of the Anura and Fishes, is not quite distinctly marked off from the auricle. It receives blood from all parts of the body except the lungs. The floor of the cavity has a large and elongated aperture leading to

the right auricle. The long axis of the oval slit is at right angles to the long axis of the heart. The sinu-auricular aperture is guarded by a pair of well developed membranous valves.

The Auricle. The right auricle is a large chamber with fairly thick walls and is situated anteriorly. The inner surface of the chamber presents a large number of muscular projections. The auriculo-ventricular aperture is situated to the left on the ventral floor at its caudal end and to the left attached to its admesial border; the right and left auricles are separated completely by a very well developed interauricular septum. The interauricular septum is not quite tensely stretched and is not quite vertical but has an oblique direction and has a slight concavity facing the right auricle. The left auricle is smaller than the right and receives blood from the lungs through the pulmonary vein which opens to it dorso-laterally. Internally there is a flap of the auricular wall which acts as a temporary valve during auricular systole. The auriculo-ventricular aperture is small and is provided with a membranous flap valve. The valves guarding the right and left auriculo-ventricular openings agree exactly with those which I have already described in Tiliqua. They are remarkable for the absence of cordae tendinae. The auricle opens into the ventricle at the ventral angle and leads to a distinct cavity of the ventricle.

The Ventricle. The cavity of the single ventricle is divided by muscular projections of its wall into a number of communicating channels which though completely separated caudally open into a common chamber at the base of the ventricle. The wall of the ventricle is very powerfully built indeed. The cavity of the ventricle presents the following main features. There projects into the cavity from the posterior apex and running dorso-ventrally a muscular ridge which divides the ventricle into two main cavities, a small left and a large right. The large right cavity is further divided by a septum, the interventricular septum into two cavities, the dorso-lateral right and the ventral cavity. The inter-ventricular septum is particularly well developed. It is attached to the ventral wall of the ventricle and has a free dorsal border anteriorly which projects freely into the cavity of the ventricle. Posteriorly the septum is continued and separates the ventral cavity effectively from the others. The ventral cavity is very clearly seen in transverse section as a deep pit and is the cavum pulmonale. The dorso-lateral cavity has therefore the incipient *left ventricle* or the *cavum arteriosum* on one side and the cavum pulmonale on the other.

The cavum venosum communicates with the cavum pulmonale round the free border of the ventricular septum. From the ventricle spring the three arteries. The three arteries are bound together by connective tissue and the term conus arteriosus has been applied incorrectly to designate the apparently single vessel. The three arteries are: the pulmonary, the left systemic, and the right systemo-carotid arteries.

The Pulmonary and the Systemic Arteries. The pulmonary artery arises ventrally from the cavum pulmoneum; the left systemic artery springs as in

Tiliqua at a short distance cranially from the origin of the pulmonary artery to the extreme right. The right systemic arises even more cranially.

The Valves. (1) *Sinu-Auricular Valves.* There are two well developed valves in the auricle guarding the sinu-auricular passage. They are attached to the cranial and caudal lips of the aperture. They are tough and membranous in character and appear to be firmly bound to the supporting wall. Though there is no fusion between the cranial and caudal valves the caudal valve overlaps the cranial valve. They come together and close the sinu-auricular passage during auricular systole.

(2) *The Auriculo-Ventricular Valves. The right auriculo-ventricular valve.* This is a large valve of a membranous character, attached to the lower end of the interauricular septum and to the wall of the ventricle. The valve slopes away from the septum, and its function is to prevent regurgitation of blood from ventricle to auricle during ventricular systole.

The Left Auriculo-Ventricular Valve. This valve also is attached to the caudal end of the interauricular septum but spreads from the septum into the walls of the ventricle. The valves on either side become a continuous membranous sheet which has its concavity towards the cavity of the ventricle. The lower free end of this valve is in a line with the ridge dividing the cavum venosum from the cavum arteriosum.

(3) *The Valves at the bases of the Arteries.* These are two large semi-lunar valves at the base of each of the three arteries. Blood in the arteries is prevented from getting back to the ventricle during ventricular diastole by the three pairs of valves.

The Course of Blood. The venous blood from the body is poured into the sinus venosus and arterial blood is poured into the left auricle. Blood from the sinus venosus passes into the right auricle by the contraction of the sinus walls. When the auricles contract, the arterial blood flows from the left auricle into the cavum arteriosum of the ventricle, and the venous blood from the right auricle flows into the cavum venosum, the two streams being directed to the sides of the ventricle by the great auriculo-ventricular valve. The venous blood gradually flows from the cavum venosum past the interventricular septum into the cavum pulmonale. When the ventricle begins to contract the blood from the cavum pulmonale flows into the pulmonary artery as its orifice is most caudally situated and the blood which fills it is under less pressure. As the ventricular contraction proceeds a part of the blood from the cavum arteriosum passes into the cavum venosum, mixes with the residual venous blood and gets into the left systemic. Finally the purely arterial blood from the cavum arteriosum passing into the cavum venosum flows past the passage into the cavum pulmonale and the left systemic and enters the right systemic artery. Thus the right systemic artery gets the oxygenated blood.

The course of blood in the heart of Eunectes is the same as in Tiliqua. Thus in Lacertilia and Ophidia the oxygenated blood from the left auricle does not flow into the cavum venosum but flows into the cavum arteriosum. I have

examined the dissected hearts of Chelonia and Crocodilia. I have reason to believe with Prof. E. S. Goodrich that the interventricular septum in Chelonia though incomplete is ventral and that the left systemic does but get a supply of mixed blood. In the Crocodilia the interventricular septum is quite complete and the left systemic and pulmonary arteries spring from the right ventricle while the right systemic comes off from the left ventricle. The right and left systemics communicate however through the *foramen Panizzae*, the exact functional significance of which is a matter for conjecture. The embryological studies of Greil establish beyond doubt that the *interventricular septum* arises ventrally. Thus the contention of Dr O'Donoghue in regard to the relation of the interventricular septum to the ventricular wall is unfortunately based on imperfect data and his statement concerning the course of blood flow in Lacertilia and Ophidia is obviously erroneous.

The results I have arrived at by a study of the Reptilian heart support the findings of Prof. Goodrich.

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ON THE CAUSATION OF CERTAIN HAIR TRACTS

By FREDERIC WOOD JONES

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A very great deal has been written upon the subject of the hair tracts of Mammals both from the point of view of their anatomical disposition and from the standpoint of the method of their formation. It is with this latter line of research that the work of Dr Walter Kidd is so notably concerned. His latest work contains what is, in the present author's opinion, the most important contribution yet made to the discussion, for throughout his writings there is expressed the idea that the hair patterns have relation to the habits and doings of the animal. Though I feel sure that he would not go so far as to declare that an animal makes its own hair patterns, it is perfectly obvious that in many instances he conceives that it is not merely the mechanical play of muscles under the skin, but the actual purposive actions of the animal itself, that produces hair trends. An example of this line of reasoning is to be found in the account of the reversed hair tract behind the rhinarium of the cat[1].

For some time past I have been examining and recording the external characters of pouch embryos of marsupials: and in the course of this work have charted the hair tracts of a fairly representative series derived from most of the families of the Didelphia (1). This work was undertaken rather from the point of view of determining certain questions concerned with didelphian phylogeny, than from any intention of inquiring into the causation of the hair tracts. The phylogenetic significance of hair tracts has been fully displayed during the course of this investigation; but the work has also forced me into embracing some rather unorthodox views which are here stated as briefly as possible.

It must be understood at the outset that these views are based only upon the examination of marsupial embryos and the study of living adults. The inquiry is limited to the available material. It must be also emphasised that in outlining my views I do not offer destructive criticism of any of the suggestions which have been put forward to account for the presence and disposition of hair tracts.

I do not contend that "friction, pressure, gravity and underlying muscular traction" are not causes of pattern production; I do not deny that the "phenomena of growth, whereby folding and other irregularities of surface are produced" are of importance, but I would add another cause, and I certainly

[1] *Initiative in Evolution*, 1920, p. 94.

think it is the most potent, and that is the animal's peculiarities in the method of conducting the toilet of the coat.

The toilet of the coat is conducted in many ways, of which the following list is probably not exhaustive.

(1) *By licking with the tongue.*

This is a conspicuous method among the *Felidae*, and I imagine that the peculiarly rough papillae of the feline tongue are better regarded as hair brushes, than, as they are so often supposed to be, instruments for rasping flesh from bone.

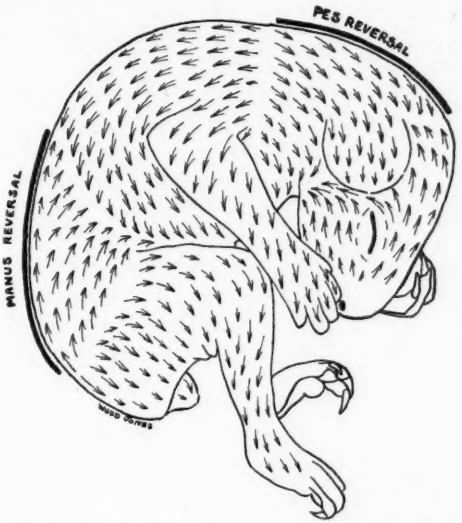

Fig. 1. Right lateral aspect of pouch young of *Phascolarctus cinereus* to show the main hair tracts.

(2) *By combing with the teeth.*

I have elsewhere (2) called attention to the function of the procumbent lower incisors and canines of the lemurs and pointed out that Cuvier so long ago as 1829 declared them to be nothing but hair combs.

(3) *By nibbling with the teeth.*

This method is adopted by many insectivorous and carnivorous animals, and it is open to question as to how far the little, sharp-pointed, front teeth of some forms are to be regarded as toilet teeth and how far as normal teeth used for the ordinary purposes of alimentation. The true polyprotodont marsupials mostly nibble their fur with their fine, sharp, front teeth and it is not until teeth of this character are phylogenetically lost that didelphians acquire the great marsupial hair comb of the syndactylous toilet digits.

(4) *By scratching with the claws or nails.*

This simple statement opens up what is in reality a vast field for the study

of structure and function. A peculiar nail or claw, often associated with a peculiarly specialised digit, is the hall-mark of a toilet digit. The condition present among the lemurs needs no discussion, the peculiar second pedal digit of *Echidna* is not so well known, and the syndactylous second and third pedal digits of those marsupials, which do not possess the many small and sharp front teeth, are often taken to be an instance of digital degeneration rather than as what they truly are, a most perfected hair comb.

Apart from the study of the specialised digital toilet implement, there is also an added complexity in the matter of scratching, for some animals scratch with the manus, some with the pes and some with both manus and pes.

(5) *By scratching with horns, by brushing with the tail, or by rubbing against external objects.*

Doubtless each of these methods leaves its mark, but as factors in the causation of hair trend of marsupials they play no recognisable part.

So much for the methods of coat toilet; it remains to determine what may be regarded as the primitive condition of the coat and what the alterations that may be effected by the toilet. It may be taken as the nearest approximation to truth to assert that in the primitive mammalian coat the hair is all directed caudad and ventrad upon the trunk and post-axially and distally upon the limbs. Several marsupials fulfil this condition and *Myrmecobius* and *Dasycercus* may be quoted as examples. It may be accepted that, where we find a reversal from this condition, the reversal has a definite functional cause, and I maintain that, in the very large number of cases, this cause is the animal's peculiarity in conducting the toilet of the coat.

To some it might seem to be an unscientific frame of mind in which to conduct an inquiry, but I certainly think that when confronted with the problem of the causation of a curious reversal in hair disposition, the possibility of solution lies in attempting to find out how the living animal can itself cause the reversal. In most cases, observation of the living animal will be rewarded with the clue to the correct solution.

It is obvious that the general build of the animal, the capacity for flexion of its various parts, the relative length of its limbs and the condition of its tongue, teeth, and manus and pes must all be taken into consideration: and the study becomes, in the main, narrowed down to an inquiry as to what parts of the body may be reached with any particular toilet implement and in what direction will this implement tend to comb or brush the hair. We will take the implements in order and see how far they seem likely to be agents in the causation of hair patterns.

(1) The tongue is not used by any marsupials, with which I am acquainted, for any extensive toilet operation. Many marsupials lick their fur in hot weather, but this is merely in order to moisten it and so to substitute the absent sweat glands. Nevertheless, many of them lick their noses after the general mammalian fashion and it is this licking which I imagine causes the well-known rhinal reversal. This is the one reversal which Dr Kidd has

ascribed to toilet operations, but he supposes it to be caused, in the cat, by rubbing the hair forwards with the paws. The paws however run so wide an area of the head and face that it seems unlikely that their action should be evidenced only in this one small tract. No marsupial has so wide a use of the tongue in toilet operations as has the cat, and in no marsupial is the rhinal

Fig. 2. Right lateral aspect of pouch young of *Wallabia greyi* to show the main hair tracts.

reversal so extensive. In *Trichosurus* the rhinal reversal and the dorsal sweep of the tongue appear to coincide, and I expect this will be found to be the case in all animals showing the hair sloping forwards immediately above the rhinarium. I know no other hair alteration caused by licking among the marsupials, but I would suggest that there are many to be found among the Monodelphia. If those having the opportunity would observe what parts of

the body any animal can, and does habitually lick, it is possible that such odd tracts as the curious groin reversal in horses, and several others, would receive their explanation.

(2) The nails and claws are extensively used by marsupials in the toilet of the coat and with many species the toilet operations bulk very large in the

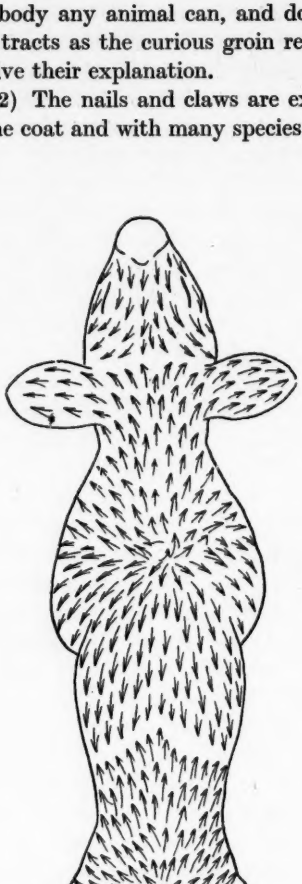

Fig. 3. *Phascolarctus.* Dorsal view of the main hair tracts.

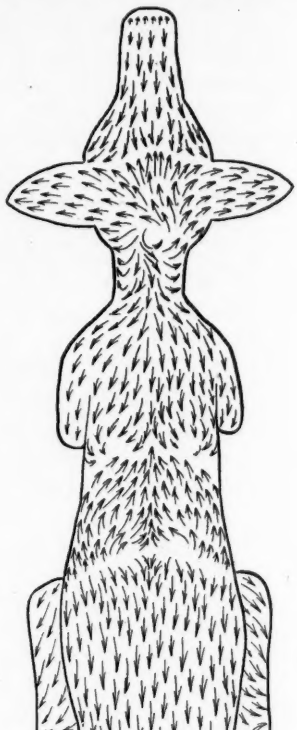

Fig. 4. *Wallabia.* Dorsal view of the main hair tracts.

occupations of the animals. I have discussed the syndactylous pedal digits elsewhere (3) and there is no need to deal further with the subject here beyond reaffirming that this curious specialisation is a highly functional one brought about for the creation of a very effective hair comb, which appears to compensate for the loss of the small front teeth in the diprotodonts, and to be aimed especially at the control of the activities of the biting lice (*Mallophaga*) which

infest the coats of marsupials. In addition to employing the syndactylous pedal hair comb, most of the syndactyla are adepts at scratching themselves with the claws of the manus. The manus and pes have their own territories of employment in the normal scratching habits of the animal, and it is easy, after some observation of the living animal, to apportion the different areas of its body as pes-areas and manus-areas: the disposition of these areas depending on the relative proportions of the body and of the anterior and posterior limbs. Even though we may plot out the whole body into pes-areas and manus-areas, there may yet be no outward evidence in the hair patterns to distinguish them. It is not until, in the habitual scratching methods of the animal, either pes or manus combs the hair in a direction reversed from the primitive hair slope that there will be a tendency to produce any change. If any animal can scratch its coat with either manus, or pes, or with both, in a direction which is caudad and ventrad no change will be produced, but there is a natural tendency in many animals, as a necessary outcome of their general build, for the scratching of the cephalic end of the body to be done largely with the pes, and for the manus to trespass on to the caudal end.

In both these cases there is a liability for the hair to be scratched the wrong way. We might therefore expect to find two common areas of reversal; a cephalic pes-reversal and a caudad manus-reversal. I think that the identification of these areas will render the study of the hair patterns of certain animals more easy of interpretation. In order to demonstrate these areas I have employed the charts of two marsupial pouch young, the charts having been drawn merely to record the hair tracts for taxonomic purposes, without any regard to the question of their causation.

The two animals figured belong to the syndactyla diprotodontia and are *Phascolarctus cinereus* and *Wallabia greyi*, animals which exhibit almost the extremes of divergent bodily proportions displayed in their section of the Didelphia. It will be seen that the hair patterns of both are complex and that, at first sight, there seems to be but little similarity between them and but little order in the disposition of the partings and reversals. Indeed, if the charts were mere diagrams, and did not represent the actual proportions of the body and limbs, it would be difficult to detect the underlying identity of the two patterns. An inspection of the figures will show that the hair tracts in the two animals are much the same but that in the long legged, short armed *Wallabia* the whole pattern is shifted cephalad.

Starting from the rhinarium there is a rhinal reversal in *Wallabia greyi* which is absent in *Phascolarctus* with its great dorsal rhinal extension. Behind that there is a normal field which in both animals extends caudad to the region of the anterior (dorsal) attachment of the auricle. Following this normal field is an area of reversal, which in *Wallabia* extends back only on to the neck and has its centre just behind the occiput, but in *Phascolarctus* ceases only on the scapular region. The occipital whorl of *Wallabia* and the

scapular whorl of *Phascolarctus* and their accompanying fields of reversal, constitute the pes-reversal areas. It is over this area that the animal is accustomed to scratch the hair the wrong way with the syndactylous pedal digits.

This is no speculative statement, for the employment of the pes in this area is constantly displayed whenever living animals are observed. The difference in extent of these areas is obviously accounted for by the relative length of the body and hind leg in the two animals. Behind the pes-reversal area is another normal tract in which the hair slopes caudad from behind the occiput to the posterior scapular region in *Wallabia*, and from the scapular region to the lower costal region in *Phascolarctus*. This normal tract is again followed by a reversal area which extends, in *Wallabia*, from the scapular to the costal region, and, in *Phascolarctus*, from the costal to the sacral region. This is the manus-reversal area; large and far back in the relatively short-bodied, long-armed *Phascolarctus*; small and far forward in the relatively long-bodied, short-armed *Wallabia*. In both animals the manus-reversal area is succeeded by the caudad normal tract.

It is perhaps not well to complicate a striking demonstration of a simple underlying principle by dragging in minor points: but a peculiar interest attaches to the ventral perineal and lower abdominal reversal area, present in *Wallabia* but absent in *Phascolarctus*. This area is also a manus-reversal area. If anyone will compare the chart of *Wallabia* with the results of a half-hour's observation of a living Kangaroo he will almost certainly obtain a demonstration of the method of formation of every one of the reversal areas figured. But of the ventral perineal reversal he is sure to see the explanation. So characteristic are the movements of the animal in producing this area that no aboriginal who plays the rôle of the Kangaroo in a corroboree would consider himself a competent actor if he did not rehearse them with considerable emphasis. If a Kangaroo can so readily demonstrate the method of formation of its hair tracts, it is likely that other animals can do the same, and it is probable that careful observation of animals, living as nearly as possible their natural lives, is capable of solving the problem of the cause of most mammalian hair patterns. I suggest that the study of a man brushing his clothes, or of a monkey scratching itself, may give the clue to the understanding of most human tracts; and I would recommend anyone to scratch his own arm and see if this simple action does not better account for the well-known antebrachial reversal than do watershed, muscular traction, gravity, or disproportionate growth theories. Although the explanation of certain hair patterns put forward here is convincing to me and may appear as plausible to others, we must not forget the somewhat far reaching consequences of adopting this thesis. Dr Walter Kidd published his views with a full sense of their Lamarckian import, and criticism has in consequence been brought to bear somewhat severely upon them. But here we have a condition in which as soon as ever hair begins to appear upon the pouch young of a marsupial, and

long before the little animal has any occasion to scratch itself, there is demonstrated the whole complexity of reversals, whorls, and partings ingrained upon the coat by no more deep-seated, life-saving or useful process than the toilet methods adopted by its ancestors. If this is not, in the old hackneyed connotation of the term, a case of acquired characters being inherited, it is difficult to conceive what circumstances could afford a satisfying demonstration of that phenomenon.

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THE HAIR SLOPE IN THE FRONTAL REGION OF MAN

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It is evident that the case for the external, mechanical and trivial causation of hair patterns is not to be won without the production of a vast amount of evidence in support of it. It is also certain that the recent authoritative paper by Professor Bolk (this *Journal*, vol. LVIII, part III, p. 206) will do much to delay the acceptance of that simple thesis, even if it does not altogether destroy belief in it.

The clear, yet elaborate, charts which illustrate Bolk's paper provide us with the best records that have yet been published of the hair patterns upon one region of the human body. The hair patterns of the frontal region of man are now recorded with an accuracy that renders discussion as to the actual disposal of the tracts unnecessary. In a previous paper, I have called attention to the importance of distinguishing between normal and abnormal tracts, or tracts in which the hair is disposed in the typical mammalian fashion and tracts in which it is reversed. Upon the human frontal region both normal and abnormal tracts are found, and, at times, the normal and abnormal tracts merge together. An abnormal tract is an entity, which at some of its borders will be sharply delimited from surrounding normal areas by a divergent parting or a whorl, but at other of its margins it may merge with normal areas by sloping convergences. Professor Bolk is dealing, in part, with an abnormal area in the human frontal region, and his figures lose somewhat in value since the whole extent of the abnormal area is not depicted, and its delimitations from the surrounding normal areas are not clearly defined. In the orthognathous human face it is easy to lose sight of the primitive mammalian landmarks, and I suggest that it is only by constantly keeping in mind the primitive and normal hair trend, that we can appreciate the abnormal. I have, therefore, preferred to illustrate the hair tracts of this region in a human foetus of 15 cm. by distorting the drawing into an orientation in which comparison may more readily be made with charts of lower mammals (see fig. 1). To Dr Walter Kidd belongs the credit of drawing attention to the great variability displayed in the disposition of human scalp hair—a variability which is not displayed anywhere on the hairy covering of any other mammal. This variability is recorded and charted by Kidd (*Proc. Anat. Soc.* 1901, p. xxx) but that paper seems to have been overlooked by Bolk. It was the very instability of scalp hair pattern that caused Kidd to postulate that it was "due to the inherited effect through numerous generations of the

method adopted in dressing the hair." Bolk has reaffirmed and extended our knowledge of this range of variability, but the conclusion he comes to from this study is opposed to the simple deductions of Kidd. According to Bolk "the great variability in the hair slope on the human forehead is a sufficient indication that mechanical influences cannot be the real factors determining the direction of the hairs" and "the hair slope is not determined by external causes."

Were it not for the fact that I have daily watched marsupials performing the toilet of their coats and, as I am convinced, rehearsing the creation of their hair trends, I should not venture to criticise this conclusion; although criticism appears to be so simple. To me it seems to be a perfectly logical deduction that the peculiar abnormal area of the human cranial hair trend,

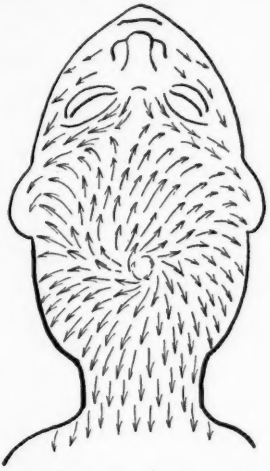

Fig. 1. Human foetus. The figure is orientated so as to render it comparable to figures of lower mammalia.

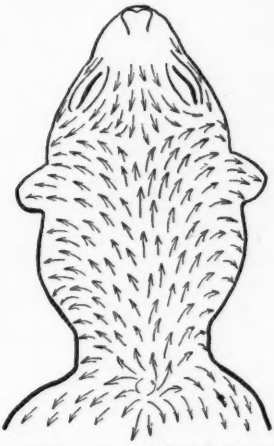

Fig. 2. Pouch young of *Pseudochirus occidentalis.*

which shows so high a degree of variability, is correlated with the most variable habit of hair dressing. The very variety in product seems to imply a variety in cause, and where else could we find so varying a cause as hair dressing? That Bolk has so clearly established this great variability may be adduced as providing fresh evidence in support of Kidd's original hypothesis. There is more multiplicity in methods of scalp scratching, hair combing, brushing and dressing among humanity the world over, than is to be found in any "more physiological" or "internal" factors postulated by Bolk. What "more physiological" or "internal" factors could be adduced which would produce this immensity of variety in a trivial manifestation of hair trend evinced in this limited, but much toileted, region?

As a matter of fact, Bolk does not suggest anything very tangible in the

way of an explanation. His summary is as follows: "The only conclusion which could perhaps with some justice be drawn from a comparison of the different conditions, is that the hair slope is not determined by external influences but that it is probably the expression of certain conditions of growth in the skin. We are still, however, entirely in the dark as to the actual connection between the process of skin-growth and the hair slope." The material used by Bolk was derived from a "population which must anthropologically be considered as a very mixed one"; and he suggests that this very racial mixing may be associated with the variability of scalp trend. In so far as mixed styles of hair dressing in males and females would be likely to contribute to the result, this speculation is probably well grounded. The suggestion that the investigation should be repeated with material derived from a purer race is one which would be well worth acting upon, especially if this purer race had a stereotyped and uniform method of hair dressing common to males and females alike. But it should not be overlooked that Kidd originally suggested the undertaking of a "statistical consideration of this matter in China."

Briefly, the abnormal scalp area, in what may be considered an average example, consists of a reversal of trend, which starts from a whorl on the vertex and passes, forwards towards the eyebrows, laterally to the temporal region and backwards to merge with the normal nuchal stream. By Bolk the abnormal area is termed the bregmatic stream. This abnormal area, as Schwalbe has shown, is absent in anthropoid apes: but according to Schwalbe's figure it is present in Tarsius and in Lemurs. It is, moreover, a common marsupial feature. In the human specimen from which my illustration is taken (as in several of Bolk's figures) there is an asymmetry of the abnormal area which manifests itself in the pattern being pushed over towards the left side of the head. This fact is probably of importance, since, to most right-handed people, parting the hair on the left side is the easiest method of hair arrangement, a fact which has not escaped Kidd's notice. In marsupial examples I find no asymmetry. In order to compare the human condition with that present in a marsupial, I have figured the head of a pouch young of *Pseudochirus occidentalis*: and by comparing figs. 1 and 2 it will be seen that there is certainly a similarity.

In the case of the *Pseudochirus*, the area is a pes-reversal, for it is made by the use of the syndactylous toilet digits of the pes. Of that I think there is no doubt whatever. In the case of man I regard it, with Kidd, as a manus-reversal, being made by the artificial toilet appliances used in the hands. Let anyone scratch his head in idleness and see if the fingers do not naturally encounter the whorl, and then traverse the stream lines forwards to the forehead, sideways to the ears, and backwards to the nape. *Pseudochirus*, with its pedal hair comb, carries the reversal further back than man does; but for the rest, the cause and the effect are similar.

TWO ANOMALIES IN THE CONSTRUCTION OF THE DIAPHRAGM

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The two examples of anomalous disposition of the muscular fibres of the diaphragm described here were noted during the present session in the dissecting room of this department. The main abnormalities affect the crura in both cases, but in both examples there are associated anomalies which are, from a practical point of view, of more importance than the mere crural variations themselves.

Case 1. *Male, aet.* 70.

In this subject the oesophagus and the aorta apparently entered the abdomen by a common opening, the oesophagus lying directly anterior to and upon the aorta. The central tendon extended farther posteriorly than usual, so that the anterior edge of the common opening was mainly tendinous, the anterior decussation being represented by only a few sparse fibres derived from the right crus.

The posterior decussation, which usually separates the oesophageal and the aortic openings, took place upon the anterior surface of the aorta at the level of the first lumbar vertebra, some two inches lower than is usual. Both crura were of approximately equal bulk, and each took an equal share in the formation of the posterior decussation, which was shaped like a flat X upon the aorta. (The right crus contribution was perhaps a little larger than that of the left crus, but the disproportion was not so great as is represented in fig. 1.)

The crura continued wholly muscular to the level of the second lumbar vertebra, and were finally inserted into the anterior common ligament on the anterior surfaces of the bodies of the second and third lumbar vertebrae and the intervening intervertebral disc.

The decussating fibres did not gain insertion with the main parts of their respective crura—instead each became tendinous, and, lying upon the surface of the psoas muscle, picked up another tendinous slip from that muscle immediately distal to the internal arcuate ligament. This formed a Y-shaped band of tendon which at the level of the third lumbar vertebra became continuous with the superficial fibres of the psoas. On the right side only this tendon gave in addition a long tendinous slip, which passed superficially to the fibres of insertion of the main crus, and was inserted into the anterior

common ligament on the anterior surface of the body of the fourth lumbar vertebra.

It is perhaps worthy of note that the coeliac axis artery arose from the aorta below the lower limit of the decussation, and that all the abdominal arteries arose at a lower level than usual. It is evident therefore that the true aortic opening was at the level of the first lumbar vertebra, and that the portion of the aorta visible from the abdomen above the muscular fibres of the posterior decussation, was in reality the lowest portion of the thoracic aorta, and not the upper part of the abdominal aorta.

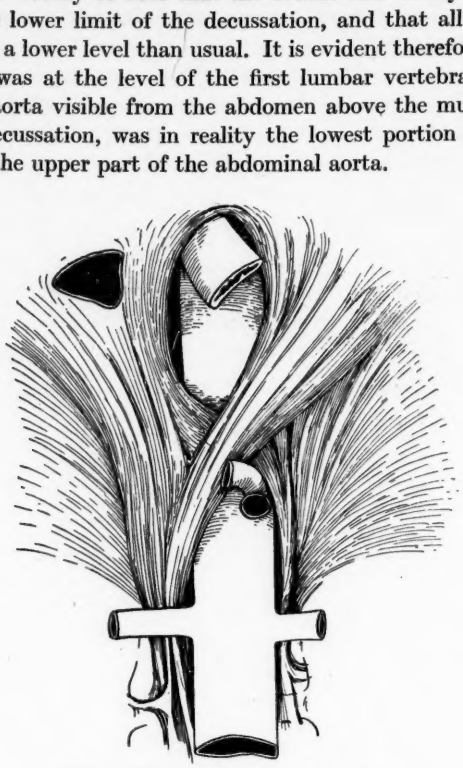

Fig. 1. Condition of the Crura in Case 1.

It is evident that in this case the abnormally low position of the posterior decussation has brought the aortic opening proper to an unusually low level. The oesophagus therefore, which appears to enter the abdomen by a common orifice with the aorta, is not really in contact with the abdominal aorta, but with an abnormally placed portion of the thoracic aorta.

Case 2. *Male, aet.* 83.

In this case the muscular separation between the oesophageal and the aortic openings was composed wholly of fibres derived from the right crus. The left crus was insignificant and was confined entirely to the left side. From the posterior edge of the central tendon, on the left side of the oesophageal opening, a rounded cord of muscular fibres, about half-an-inch by an inch in section, passed between the oesophagus and the aorta to join the upper fibres

of the right crus on the right side of the aorta. The right crus, which was unusually thick and fleshy, was inserted by a short, thick, twisted mass of tendinous fibres into the anterior common ligament on the anterior surface of the body of the third lumbar vertebra. The left crus, much smaller than the right, gained insertion to the anterior surface of the upper border of the second lumbar vertebra.

This interesting variation was accompanied by a further deficiency of the left half of the diaphragm. A semicircular gap of about two inches radius was left in the posterior abdominal wall above the last rib and the site of the

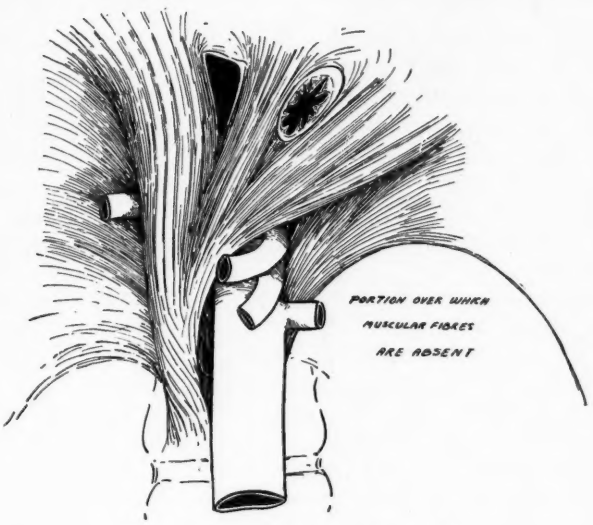

Fig. 2. Condition of the Crura in Case 2.

external arcuate ligament, which was absent on this side. Muscular fibres were inserted normally on to the internal arcuate ligament, and then arched over to be inserted to the eleventh and twelfth ribs, leaving a semicircular gap lined only by pleura. Directly attached to this "abdominal" layer of the parietal pleura was extra-peritoneal fatty tissue (the so-called "transversalis fascia"). Owing to the post-mortem shrinking of the formalin-hardened lungs, the eleventh and twelfth ribs were plainly visible from the abdomen through both layers of the parietal pleura.

The enlarged right crus was pierced by the right renal artery. This vessel arose at a higher level than its fellow of the opposite side and for about an inch was entirely covered by the muscular fibres of the crus. The left renal artery arose at its normal level and passed in front of the small portion of tendon of the left crus which extended to the body of the second lumbar vertebra.

This case therefore appears to be an example of a congenital deficiency of the left side of the diaphragm, which manifested itself by an actual gap in the musculature of the left cupola and in an incomplete development of the left crus. The deficiency in the left side was partly compensated for by an hypertrophy of the diaphragmatic element derived from the right crus. It is rather remarkable that despite the large gap in the musculature of the left cupola, there was no suggestion of visceral displacement: the deficiency had not been accompanied by any hernia.

Figs. 1 and 2 which illustrate this paper have been drawn for the author by Dr Wood Jones, Elder Professor of Anatomy in the University of Adelaide.

TORTUOSITY OF THE CERVICAL SEGMENT OF THE INTERNAL CAROTID ARTERY

By JOHN CAIRNEY, M.B., Ch.B.

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That the cervical portion of the internal carotid artery may in some cases be tortuous is mentioned in the recent editions of most of our standard text-books, usually in small type under the heading of peculiarities or of variations. The statements to be found in Gray (22nd edition, 1923) and Piersol (7th edition, 1919) may be mentioned as typical: according to Gray, "The course of the artery, instead of being straight, may be very tortuous"; according to Piersol, "In its cervical portion the internal carotid occasionally takes a somewhat sinuous course, and, especially in its upper part, may be thrown into a pronounced horseshoe-shaped curve."

A rather greater frequency than these statements imply is indicated by some of the earlier descriptions. Thus Hart, who wrote the article on the carotid artery in Todd's *Cyclopaedia* nearly 90 years ago, appears to have regarded a tortuous condition of the internal carotid in its cervical portion as normal; according to his description, the artery "mounts upwards and forwards in front of the three superior cervical vertebrae, and making a few contortions along the side of the pharynx, enters the foramen caroticum of the temporal bone." Harrison, about ten years later, accepted tortuosity as the rule rather than the exception; describing the internal carotid artery (*The Dublin Dissector*, 5th edition, 1847), he says: "This vessel, through its entire course, is remarkable for its tortuosity; in the neck it is very variable in this respect, but is generally bent into several curves." In this connexion it is interesting to note that certain text-books in other languages, for example, Poirier and Charpy and Rauber-Kopsch, in contrast to those in English, still describe a sinuous course of the artery as the normal.

Certain of the older text-books, in discussing tortuosity of the internal carotid, refer to actual cases which had been observed. Quain (6th edition, 1856) describes a case in which the artery "was observed, after having reached nearly to the base of the skull, to turn downwards for more than an inch, and then abruptly to ascend again, being thus twice closely curved or folded on itself." Ledwich (*The Practical and Descriptive Anatomy of the Human Body*, 1877) mentions an instance of "a very peculiar course of the internal carotid," which consisted in a similar though longer tortuosity. Certain of the clinical journals contain descriptions of further cases, among them being

those recorded by Edington (1901), Rowlands and Swan (1902), Smith (1902), Fisher (1915), and Schaeffer (1921).

CASES OF TORTUOSITY OF THE INTERNAL CAROTID ARTERY OBSERVED IN THE ADULT

The question of tortuosity of the internal carotid artery first came under my notice about eighteen months ago, and since that time I have personally examined these vessels in every subject that has been dissected in this department. The observations now extend over five terms, during which the head and neck have been dissected in 36 subjects. Of these, 10 showed definite tortuosity of the cervical portion of the internal carotid on one or both sides; in 2 subjects the condition was bilateral, while in the remaining 8 it was unilateral, existing on the right side in 6 cases, and on the left side in 2. Thus, of 72 internal carotids examined, 12 were found to be definitely tortuous. The main facts of these cases are indicated in Table I, the cases being numbered in the order of their occurrence; the specimens themselves are depicted (as seen from in front) in fig. 1, the number of the case being noted beneath each.

The examination of these specimens shows that in each case the tortuous segment of the vessel consists of two bends, which for convenience in reference

Table I

Case No.	Age	Side on which tortuosity present	Plane of tortuosity	Bend which is medial	Relation to pharynx and tonsil
1	83	Right	Approximately midway between sagittal and coronal	Second	Region of second bend is nearer pharynx than usual position of the artery, but the part of the pharynx to which it approaches is above and behind the tonsil
2	84	Right	First bend forwards in sagittal plane; second in coronal plane	Second	Ascending limb of second bend in contact with pharynx just above upper pole of tonsil
3	78	Right	Approximately midway between sagittal and coronal	First	The portion of the artery ascending to the first bend is in contact with the pharyngeal wall for about 1 cm. in region of tonsil
4	76	Right	Approximately midway between sagittal and coronal	First	The portion of the artery ascending to the first bend is in contact with the pharyngeal wall for about 1 cm. in region of tonsil
5	73	Right	First bend in coronal plane; second backwards in sagittal plane	Second	Junction of first and second bends is nearer pharynx than usual position of the artery, but the part of the pharynx to which it approaches is a short distance above upper pole of tonsil
6	78	Right	First bend forwards in sagittal plane; second in coronal plane	First	The portion of the artery ascending to the first bend is nearer pharynx than the usual position of the artery, opposite upper pole of tonsil
7	Old age	Both	On right side: first bend in coronal plane; second backwards in sagittal plane	Second	Medial aspect of second bend almost in contact with pharynx, a short distance above upper pole of tonsil
			On left side: first bend forwards in sagittal plane; second in coronal plane	Second	Ascending limb of second bend almost in contact with pharynx about 1 cm. above upper pole of tonsil
8	Old age	Left	First bend in coronal plane; second backwards in sagittal plane	Second	No part nearer pharynx than usual. (Tortuosity just below base of skull and entirely lateral to carotid canal)
9	72	Left	Approximately midway between sagittal and coronal	Second	No part nearer pharynx than usual. (Tortuosity just below base of skull and entirely lateral to carotid canal)
10	69	Both	On both sides: first bend forwards in sagittal plane; second in coronal plane	Second	On both sides, ascending limb of second bend in contact with pharynx for about 1 cm. on left side in region of tonsil, and on right side just above tonsil

we may term first and second, or proximal and distal, taking them in order as we follow the vessel along its whole length from its origin to its entrance into the carotid canal.

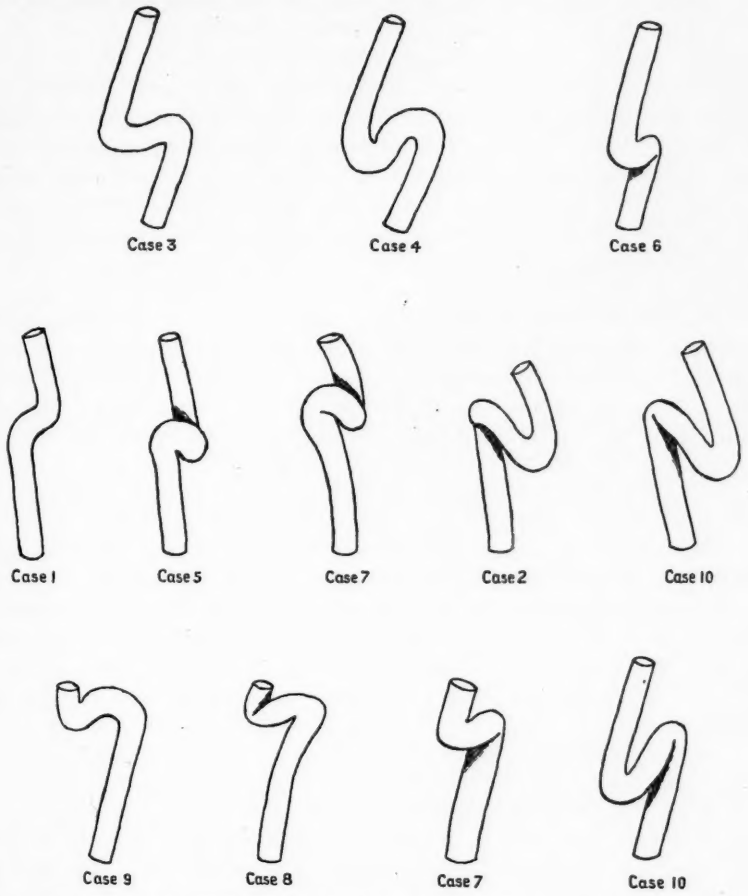

Fig. 1. Tortuous internal carotids in the adult (seen from in front).

Upper row: cases in which the first bend is medial; all specimens from right side.
Middle and lower rows: cases in which the second bend is medial; middle row are specimens from right side, lower row from left side.

In the cases which I have seen, the plane of the tortuous segment of the artery varies, three types being recognisable: in the first type, the tortuosity lies all in one plane, approximately midway between sagittal and coronal (cases 1, 3, 4 and 9); in the second type, the first or proximal bend is in the coronal plane, while the second or distal bend is backwards in the sagittal

plane (cases 5, 7 on the right side, and 8); in the third type, the proximal bend is forwards in the sagittal plane, while the distal bend is in the coronal plane (cases 2, 6, 7 on the left side, and 10). In all of these types one bend is in every case situated medial to the other; viewed as a series, however, the cases show some instances in which the first bend is the medial one and others in which the second bend is medial. In fig. 1, those specimens in which the first bend is medial are shown in the upper row, while in the other two rows are included those specimens in which the second bend is medial to the first.

With regard to the plane of the tortuosity, it should be noted that, while only the three types mentioned were observed in the present series, other types have been described. Fisher (1915) describes a case in which the tortuosity (present on both sides) was entirely in the sagittal plane, and quotes a case recorded by Stimson, in which a tortuosity near the origin of the vessel lay in the horizontal plane; while from the study of the literature it appears evident that cases have also occurred in which the tortuosity was entirely in the coronal plane. The case recorded by Smith (1902) is peculiar in that the vessel formed a complete circular coil.

THE RELATION OF THE NORMAL AND THE TORTUOUS INTERNAL CAROTID ARTERY TO THE PHARYNX AND THE TONSIL

Although it is now definitely established that the internal carotid artery normally lies behind and lateral to the tonsil and separated from it by an interval of about an inch, reference to earlier editions shows that some at least of our standard text-books have passed through a stage in which the internal carotid was described as lying directly lateral to the tonsil, separated from it only by the superior constrictor muscle of the pharynx. Of this fact Gray's *Anatomy* forms an interesting example. In the 11th edition (1887), the internal carotid is mentioned in three separate places as lying directly lateral to the tonsil: firstly, in the description of the artery; secondly, under the heading of the surgical anatomy of the artery; and thirdly, in the description of the tonsil. The 16th and 17th editions show these three separate statements in process of emendation. In the 16th edition (1905), in the description of the artery the tonsil is mentioned as one of the medial relations, and this relation is emphasised under the heading of surgical anatomy; in the description of the tonsil, however, the artery is stated to lie "behind and to the outer side of the tonsil, and nearly an inch (20 to 25 mm.) distant from it." In the 17th edition (1909), the statement under the heading of the surgical anatomy of the artery has also been corrected, with the result that only in the description of the artery does the former inaccuracy remain; in the more recent editions the discrepancy has been removed by the omission of the tonsil from the list of the medial relations of the artery. Quain's *Elements of Anatomy* shows a similar change; in this case, however, the relation is mentioned in only two places, and both statements are corrected in the 10th edition (1892 and 1896). Morris's *Human Anatomy* still shows a

discrepancy similar to that which existed for a time in Gray: in the 6th edition (1921) the artery is still described as being in relation on its medial side with the tonsil (separated by the superior constrictor), while a similar statement in the description of the tonsil was corrected in the 2nd edition (1898).

In the description of the tonsil in Poirier and Charpy, the correct relation of the artery to the tonsil is stated to have been demonstrated by Otto Zuckerkandl in 1887. The fact, however, that the artery is normally some distance away from the tonsil appears to have been known to English writers at least fifty years previously; thus Hart, in his description of the artery in Todd's *Cyclopaedia* (1835–1836) states that the artery lies external and posterior to the tonsil "at a distance of from six to eight lines in the natural state of the parts"; while Harrison, in his description of the tonsil in the *Dublin Dissector* (5th edition, 1847), states that "the internal carotid artery is posterior and somewhat external to it," and that the tonsil is separated from the artery "by the superior constrictor and by a considerable interval filled by cellular tissue." Among the French authorities, Cruveilhier (Tome II, 5th edition, 1874–1876), in describing the tonsil, mentions the relation of the internal carotid to it as follows: "Un rapport important est celui qu'elle affecte avec la carotide interne, mais ce rapport est très-éloigné."

That the internal carotid may sometimes be wounded during operations on the tonsil is mentioned by various authorities, the earliest reference to such a possibility in the literature at my disposal being in the article by Hart, who describes it as "an occurrence of which the records of experience are not without examples." During the stage in which the internal carotid was described as lying directly lateral to the tonsil, the explanation of such cases appeared obvious; thus Gray through several editions emphasises the practical importance of such a relation on the ground that "cases have occurred in which the artery has been wounded during the operation of scarifying the tonsil and fatal haemorrhage has supervened." In more recent years, since the normal position of the artery relative to the tonsil has become generally recognised, the text-books of surgical anatomy have in consequence come to regard any damage to the internal carotid during operations on the tonsil as a rather unlikely accident. The following sentence, occurring in the recent editions of Treves and Keith's *Surgical Applied Anatomy*, probably represents an accuarte statement of the general opinion to-day: "The vessel is, indeed, about $\frac{4}{5}$ of an inch posterior to that body, and is in comparatively little danger of being wounded when the tonsil is excised." A more extreme view is advanced by Campbell in his text-book of *Surgical Anatomy* (3rd edition, 1921): "The source of tonsillar haemorrhage is worthy of consideration since the internal carotid artery continues, in the minds of some operators, a possible factor in tonsillar haemorrhage....It is impossible to injure the internal carotid artery in tonsillotomy." Campbell's statement to the contrary, cases certainly have occurred in which, during the operation of tonsillectomy, skilled operators have wounded the internal carotid artery with fatal results; one such case

is referred to in the Paris letter of the *Journal of the American Medical Association* for February 19th, 1921; the patient was a young girl, and the operation was performed by an expert surgeon; "a judicial necropsy was held, and a large tear was discovered in the internal carotid artery."

The most reasonable explanation of the occurrence of such cases appears to consist in the recognition of tortuosity of the internal carotid as a factor in bringing the vessel nearer the pharyngeal wall—in the words of Schaeffer (1921), "occasional marked sigmoid tortuosity of the cervical segment of the internal carotid artery, whereby the vessel is forced into intimate topographic relationship with the palatine or faucial tonsil, the usual distance of 2·5 cm. between the tonsil and the artery being obliterated." This view, it may be noted, is not by any means new. It is mentioned by Cruveilhier (Tome III, 5th edition, 1877), and is well expressed by Testut (Tome II, 4th edition, 1900) as follows: "La carotide interne, généralement rectiligne, peut être plus ou moins flexueuse et décrire ainsi des courbes très variables par leur nombre, leur direction, leur étendue; l'une de ces courbes vient parfois se mettre en rapport avec la face externe de l'amygdale, dont l'ablation peut, dans ces cas, être fort dangereuse." Tortuosity as a factor in bringing some portion of the artery nearer the tonsil than usual was recognised by Harrison (1847), according to whose description the internal carotid artery is posterior and somewhat external to the tonsil, "and, when tortuous, very near to it"; and also by Macalister (1889) who, in describing the tonsil, wrote: "When the internal carotid artery is tortuous it lies close to its hinder and outer surface, separated therefrom by the superior constrictor muscle of the pharynx."

In the twelve cases of tortuosity of the internal carotid artery which I have observed in the adult, there were only two in which some part of the tortuous segment was not brought nearer the pharyngeal wall than the usual position of the artery; in these two instances, the tortuosity was situated just below the base of the skull and entirely lateral to the carotid canal. In the remaining ten cases, the plane of the tortuosity was such that the most medial portion of the tortuous segment was in all cases not only medial but also ventral to the usual position of the artery, in this way approaching, and in some cases coming actually in contact with, the pharyngeal wall.

In this series of cases, there are three in which the artery comes to lie directly lateral to the tonsil for an appreciable distance (in each case about 1 cm.), only the superior constrictor intervening; these are no doubt cases in which during life pulsation might have been left in the tonsillar field, and the position of the vessel might have added an element of risk in operations on the tonsil. It is, however, evident that the occurrence of tortuosity does not of necessity imply an intimate relation of the tortuous segment to the tonsil. Thus the observations of Kelly (quoted by Fisher, 1915) appear to show that, when the tortuosity is entirely in the coronal plane, it may cause pulsation not in the lateral wall but in the dorsal wall of the pharynx. Again,

the level of the tortuosity is an important factor in determining the relation of the artery to the tonsil; in my series, the majority of the vessels show tortuosity at a level which is entirely above the upper pole of the tonsil. In this connexion, the question of whether the proximal or the distal bend is the one nearer the pharynx assumes importance; thus, in cases 3 and 4, in which the first bend is medial, the portion of the vessel ascending to that bend lies directly lateral to the tonsil, while in case 2, in which the second bend is medial, the portion of artery ascending from that bend lies entirely above the tonsil. The lateral extent of the tortuous segment is also worthy of note; in certain of the cases recorded here, the tortuous segment did not come into contact with the pharyngeal wall but remained separated from it by an interval.

CAUSATION OF TORTUOSITY OF THE CERVICAL SEGMENT OF THE INTERNAL CAROTID ARTERY

Speaking generally, one may say that two views have been advanced to explain the occurrence of tortuosity of the cervical portion of the internal carotid: (1) the older view, favoured by Edington (1901), Rowlands and Swan (1902), and Moorhead (1902), to the effect that the condition is in all cases entirely due to arterio-sclerosis and increased arterial pressure occurring either in old age or as a result of disease such as chronic nephritis; (2) the more modern view, advanced by Fisher (1915) and by Schaeffer (1921), to the effect that the condition is congenital and probably represents a reversion to a more primitive type. From the clinical standpoint, the question of which of these opposing theories is correct is no doubt of considerable importance.

The older theory appears to have been the natural outcome of the fact that cases of tortuosity were observed entirely in dissecting-room subjects, in whom, on account of their advanced years, sclerosis of the arteries may safely be assumed in the majority of instances. For this reason the condition of tortuosity appears to have been regarded as nothing more or less than a condition likely to be seen more or less frequently in old age, a view that still finds a place in the latest edition of Morris's *Anatomy*. In the case recorded by Edington (1901), the age of the subject was only 34; the cause of death was, however, certified as chronic Bright's disease, and this fact led Edington to express the opinion that the condition "might perhaps be associated with the arteritis of chronic nephritis."

The fallacy of reasoning entirely from the ages of dissecting-room subjects in whom a tortuous condition of the artery is found was first pointed out, I believe, by Fisher (1915); in the majority of cases the subjects in whom tortuosity is present are no older than those in whom the condition is absent, and the dissecting-room as a rule offers little opportunity for making observations on younger individuals. In both of the cases which Fisher himself observed, sections of the vessels were examined microscopically, and were reported as showing that the evidence of atheroma was very slight indeed and quite insufficient to account for the tortuosity. In all the cases which

I have seen, there was certainly a complete absence of any visible and palpable change in the wall of the vessel such as one commonly sees in other arteries (e.g. the tibial and the radial) which have become tortuous; only one specimen was sectioned for microscopical examination, and in this case, though sclerosis could definitely be detected, it appeared insufficient to account for the marked tortuosity of the vessel. It must, I admit, be conceded that in the case of the cervical portion of the internal carotid, on account of the fact that the succeeding portion of the vessel is fixed in the carotid canal, less degenerative change might permit tortuosity to be produced than in the case of other arteries; on the contrary, however, I would suggest that to demonstrate arterio-sclerosis in a tortuous internal carotid from a subject of advanced years is after all of little value as evidence, since it is impossible to state whether the sclerosis is responsible for the tortuosity or whether it is merely an old-age change occurring in an already tortuous artery.

The evidence on which the more modern theory is based appears to consist in the main of the observation of pulsating vessels in the pharynx in the living subject. Fisher quotes Kelly as having shown that the presence of large pulsating vessels in the posterior wall of the pharynx in four cases was due to tortuosity of the internal carotid artery; one of the patients (in whom the condition was bilateral) was aged 22; Kelly's reasoning appears to have been based on the resemblance in shape and size between the tortuous vessels seen in the pharynx and tortuous internal carotids in a museum specimen. Schaeffer (1921) mentions Farlow as having observed large pulsating arteries in the pharynx, which he believed to be internal carotids, in patients as young as 14 years, and Wood as having reported similar large pulsating vessels in two children aged 5 and 7 years respectively.

In the hope of possibly supplying a little further evidence on this question, I recently dissected the internal carotid arteries in 20 foetuses of ages ranging from about five months to full term. Of these, four showed definite tortuosity of the cervical portion of the internal carotid, and in one instance the condition was bilateral, making a total of five cases of tortuosity in 40 internal carotids examined. The specimens from these cases are shown in fig. 2. This

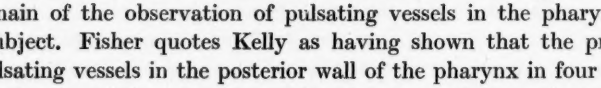

Fig. 2. Tortuous internal carotids in the foetus.

investigation certainly indicates that tortuosity of the vessel is not by any means limited to old age, but that, on the contrary, in some cases at any rate it is congenital. Whether the condition is as frequent in the young as in the old I am not in a position to state; while my personal observations show a

fairly close correspondence between the proportion of tortuous internal carotids in the foetus and the proportion in the adult of advanced years, the numbers of each class examined have been relatively few, and the examination of a much larger series would be necessary in order to provide figures on which further reasoning might safely be based.

If then it is admitted that in some cases (if not in all) the occurrence of tortuosity is congenital, we have still to enquire in what manner and due to what factors the tortuous condition of the vessel becomes developed. Fisher suggests that the explanation is to be found in the study of comparative anatomy; he points out that in many mammalia the internal carotid is more tortuous than in man, and quotes Chauveau's statement to the effect that in the seal the carotid artery is nearly forty times longer than the distance it has to traverse; from such considerations he concludes that "it would be surprising if we did not meet with great tortuosity of the internal carotid artery as a congenital abnormality in man." In the human subject, so far as I can ascertain, no reference to embryology throws any particular light on the condition.

SUMMARY AND CONCLUSIONS

1. Tortuosity of the cervical portion of the internal carotid artery is a condition which was definitely recognised at least nearly 90 years ago, and in most of our standard text-books is briefly mentioned as being occasional in its occurrence. Individual cases have been described by a number of observers, and twelve further instances, seen in the examination of 36 dissecting-room subjects, are presented here.

2. In the great majority of cases, the internal carotid artery when tortuous approaches nearer to the pharynx than its usual position, and in some instances comes to lie actually in contact with the dorsal or the lateral pharyngeal wall. In a certain proportion of such cases, but by no means in all, the artery becomes a directly lateral relation of the tonsil, only the superior constrictor intervening.

3. Cases have been observed in life, not only in adults but also in children, in which pulsation in the dorsal or the lateral pharyngeal wall has probably been due to tortuous internal carotid arteries, while the occasional relation of such a vessel to the tonsil no doubt explains the fortunately rare cases in which the internal carotid artery has been wounded by skilled operators during the operation of tonsillectomy.

4. A tortuous condition of the cervical portion of the internal carotid artery is, in some instances at least, congenital, as is shown by the observation of five instances in the examination of these vessels in 20 foetuses; but whether all cases occurring in subjects of advanced age are explainable on the hypothesis of the condition being congenital requires a much larger series of cases to determine.

In presenting these observations, I desire to record my thanks to Prof.

W. P. Gowland for permission to publish the cases which have occurred in the dissecting-room of this department, and for authority to examine the internal carotid arteries in a certain number of foetuses.

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ON A PROBLEMATICAL ORGAN IN THE LAMPREY

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WHILE engaged in studying the development of the hypophysis in Petromyzon my interest was aroused by a prominent vesicular organ situated in the olfactory capsule, a structure of such dimensions and so extraordinarily vascular, that it could not fail to attract attention. As far as I know this organ was first noticed by Scott (8) studying the development of Petromyzon, and it was figured by him as a few vesicles situated in the postero-ventral region of the olfactory capsule. He was unable to find any connexion between the cavities of the vesicles and the olfactory organ or the hypophysial cavity. He regarded the organ as of doubtful significance but probably homologous with Jacobson's organ of the higher chordates.

Pogojeff (7) investigating the histology of the nose was led to regard the organ as a gland, as was also von Kupffer (3). Lubosch (4, 5), however, denied its glandular nature and considered it to be part of some rudimentary organ. Ballowitz (1) regarded the vesicles as glands and described them as opening into the cavity of the olfactory organ by fine ducts. Peter (6) denies the possibility of Scott's hypothesis, that they represent Jacobson's organ. Woerdeman (10) considered the possibility of their representing the lobuli laterales or pars tuberalis of the pituitary body of higher chordates. Elsewhere I have given reasons for thinking this improbable (de Beer (2)). Other observers have given passing notice to these organs without figuring them: they will not be enumerated here since references to them are to be found in Lubosch's work (5).

In view of the diversity of opinion of previous observers not only as to the morphological significance of these organs but also as to their function, and of the fact that some of their descriptions and figures did not answer to my observations, it seemed advisable to re-investigate the matter. Accordingly the present paper aims at giving a description of the morphology and development of the organs. The work was done on material of *Petromyzon planeri* collected at Naples in 1922 and *P. fluviatilis*, and carried out in the Department of Zoology and Comparative Anatomy at Oxford. I must thank Prof. Graham-Kerr and Prof. Hill for kindly giving me references to some of the literature.

A transverse section through the olfactory capsule of an adult *Petromyzon planeri* posterior to the involutions of the olfactory epithelium shows the

organ as in fig. 1. It is composed of an aggregation of vesicles separable into two masses by a more or less well-defined partition containing pigment cells. The masses themselves are surrounded by pigment cells which abound in the olfactory capsule. The vesicles are more or less circular in section; in some cases the cavities of adjacent vesicles may communicate with each other, but not with any other organ or cavity.

Most striking is the dense crowd of cells closely surrounding the vesicles and which from their structure, size and staining reactions are nothing other than blood corpuscles. Fig. 1 does not convey an adequate impression of

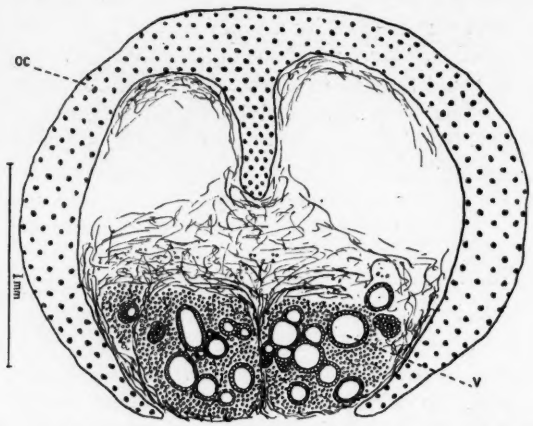

Fig. 1. Transverse section through the posterior region of the olfactory capsule (of P_1 *planeri*) showing the paired main groups of vesicles. ×30.

bc., blood corpuscles; *ca.*, carotid artery; *cine.*, cavity of involution of the nasal epithelium; *cn.*, cavity of the nose; *d.*, diverticula of the nasal epithelium which will give rise to vesicles; *fb.*, forebrain; *hc.*, hypophysial cavity; *hs.*, hypophysial strand leading to Pituitary; *n.*, nerve to vesicles; *oc.*, olfactory capsule; *oe.*, olfactory epithelium; *on.*, olfactory nerve; *p.*, pituitary body; *pc.*, pigment cells; *s.*, median septum of the nose; *tc.*, *Trabeculae cranii*; *ul.*, upper lip; *v.*, vesicles.

their numbers since it is impossible to draw them packed tightly enough. There are no well-marked blood vessels in this region, and the corpuscles lie in large irregular sinuses in which the vesicles of the organ are bathed. This close association of the organ with blood corpuscles must be of importance, and be considered when dealing with the function and significance of the organ.

A transverse section further forward through the olfactory capsule cuts the involutions and folds of the olfactory epithelium. The organ is found to consist of isolated bunches of vesicles, each bunch in contact with the bottom of a fold of the olfactory epithelium (fig. 2). Some of the more ventral bunches are continuous posteriorly with the large masses shown in fig. 1. They are all closely surrounded by blood corpuscles, and pigment cells form a loose

revetment round them. Branches of the olfactory nerve are shown in black and some branches are distributed to the bunches of vesicles.

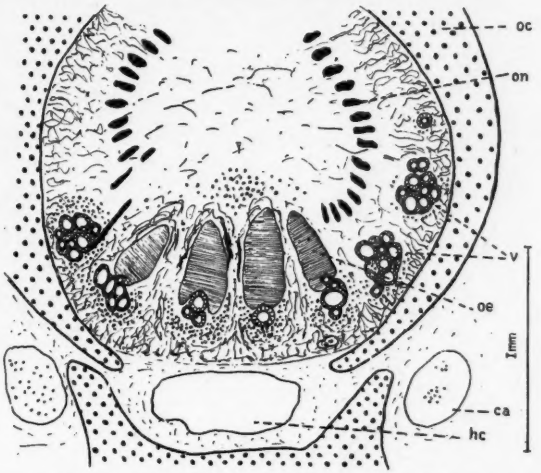

Fig. 2. Transverse section anterior to Fig. 1. The bunches of vesicles are apposed to folds of the olfactory epithelium. ×30.

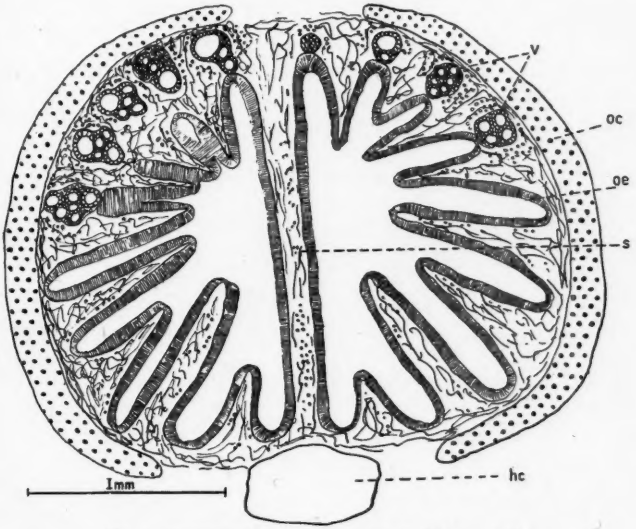

Fig. 3. Transverse section anterior to Fig. 2. ×30.

Although the bunches are in contact with the olfactory epithelium the cavities of the vesicles do not communicate with the olfactory cavity or any other structure.

Still further forward, fig. 3, the more dorsal involutions of the olfactory epithelium are cut, and groups of vesicles are found in contact with these also. The ventral involutions have no vesicles attached to them in this section.

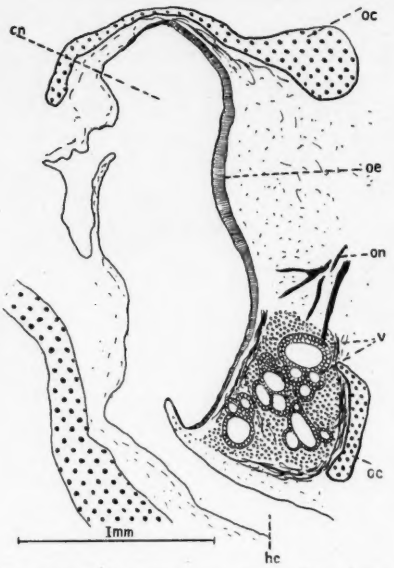

Fig. 4. Sagittal section near the median plane, showing the relations of the organ to the olfactory and hypophysial cavities, and nerves. ×30.

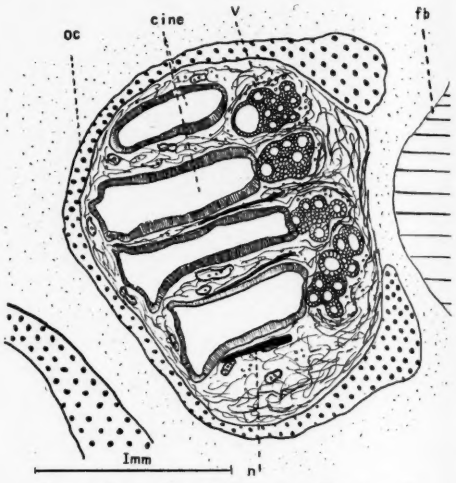

Fig. 5. Sagittal section lateral to Fig. 4. ×30.

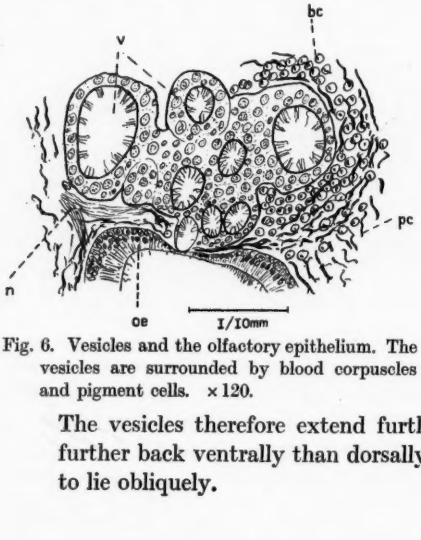

Fig. 6. Vesicles and the olfactory epithelium. The vesicles are surrounded by blood corpuscles and pigment cells. ×120.

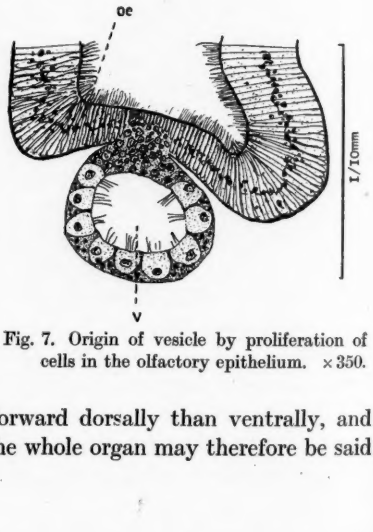

Fig. 7. Origin of vesicle by proliferation of cells in the olfactory epithelium. ×350.

The vesicles therefore extend further forward dorsally than ventrally, and further back ventrally than dorsally. The whole organ may therefore be said to lie obliquely.

In longitudinal vertical section the organ appears as in fig. 4, which is taken slightly to one side of the middle line and consequently of the dorsal aperture of the olfactory cavity which appears closed. In the postero-ventral corner of the olfactory capsule the main mass of vesicles is seen in its dense cloud of blood corpuscles. This section also shows some of the branches of the olfactory nerve distributed to the vesicles. It is clear that the vesicles have no communication with the olfactory cavity or the hypophysial cavity.

Further laterally a longitudinal vertical section cuts through folds of the olfactory epithelium (fig. 5). The vesicles are here seen to be grouped into bunches apposed to the posterior ends of the involutions of the olfactory epithelium (see figs. 2 and 3). They extend laterally almost as far as the cartilaginous lateral wall of the olfactory capsule.

Nowhere do the vesicles come into contact with any structure except the olfactory epithelium. Fig. 6 shows a high power view of a bunch of vesicles and a portion of the olfactory epithelium. It has been stated by Ballowitz (1) that the cavities of the vesicles communicate with the lumen of the olfactory organ by means of fine ducts. As a result of tears in the sections such appearances may and do occur, but I have never observed any such connexion in the adult lamprey which I did not believe was due to an artefact, and I think that the vesicles are closed. This is also the opinion of Lubosch (5). It becomes necessary therefore to explain the intimate topographical relations between the dorsal and lateral bunches of vesicles and the olfactory epithelium; the central masses of vesicles shown in figs. 1 and 4 do not enter into relation with it. There can be no doubt that it is due to the fact that these dorsal and lateral groups of vesicles are budded off from the olfactory epithelium at the ends of its involutions (fig. 7). I will return to this matter when dealing with the development of the organ, it suffices here to say that the correspondence between the bunches of vesicles and the olfactory involutions is due to the fact that the former are produced by proliferation of cells of the latter, but that there is no other connexion between them. Those vesicles which have been definitely formed are separated from the epithelium by a well-marked limiting membrane (fig. 6); vesicles in process of formation are still attached to the olfactory epithelium.

The histology of the vesicles is interesting. The cavity which contains a coagulated fluid is lined by a layer of large cells, more or less cuboidal in shape, tending to taper to a point directed away from the lumen of the vesicle (fig. 8). These cells contain a well-defined nucleus with the chromatin dotted about. The nucleus occupies a basal position in the cell with regard to the lumen. The cytoplasm is granular; but the most striking feature of these cells is the possession of cilia directed into the cavity of the lumen.

From the fact that some authors have attributed a glandular nature to the organ it became necessary to enquire as to whether these cells showed the histological characters of glands. By appropriate staining methods this can be demonstrated. Fig. 9 is drawn from a preparation stained with iron

haematoxylin and well differentiated. In each of the large cells a dense crowd of granules is to be seen between the nucleus and the free edge of the cell, bordering on the lumen of the vesicle. These granules might be taken for a group of mitochondria were it not for the fact that the material was fixed in corrosive sublimate and acetic acid. The granules can also be seen when the preparations are stained with safranin and lichtgrün, but not with Ehrlich's haematoxylin and eosin, borax carmine and picronigrosin or methyl blue and eosin. It was thought that the granules might be of the nature of mucin, and accordingly some preparations were stained with Mayer's mucicarmine. Although some of the contents of the vesicles, granules here and there, appeared to take up the stain, the granules in the cells may definitely be said not to be mucin. The efficacy of the mucicarmine had previously

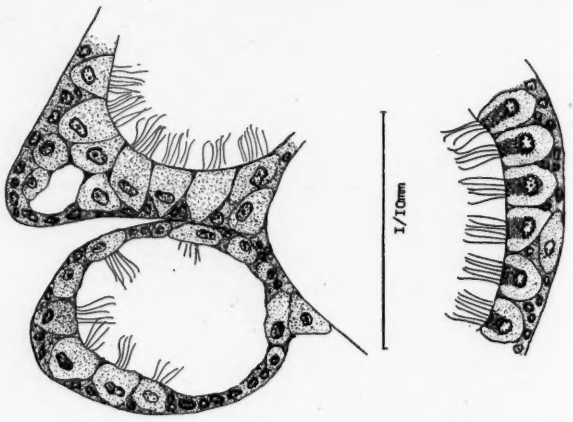

Fig. 8 Fig. 9

Fig. 8. Histology of the vesicles. Large glandular ciliated cells, and small interstitial cells. ×350.
Fig. 9. Glandular cells stained with iron haematoxylin showing granules. ×350.

been tested with glands of known mucinogenous nature. Thionin and toluidin blue which give metachromatic stains with mucin, were tried but without result. The conclusion is that these cells secrete a substance which is not mucin, in the form of granules. These granules are formed in connexion with the nucleus and are evacuated into the cavity of the vesicle.

Besides these large glandular cells the vesicles consist of small cells wedged in between the larger ones. Their nuclei are distinct and their cytoplasm is dense. They are probably to be regarded as indifferent elements. The membranes lining the inside and outside of the vesicles are smooth. The cavity of the vesicles contains a coagulated fluid which presumably escapes from the vesicles through the lymph clefts between the cells, as is the case with the thyroid.

DEVELOPMENT

In a larva of *Petromyzon planeri* 35 mm. long the olfactory invagination is well formed, and by the great expansion of the upper lip comes to lie in a depression opening to the exterior by the median dorsal aperture (fig. 10). The glands of the pituitary body are beginning to differentiate but there is as yet no true hypophysial cavity. The hypophysial tissue extends as a solid strand from the cavity of the external depression to the glands.

At the postero-ventral extremity of this depression the olfactory epithelium shows a number of inpushings or diverticula, represented under higher magnification in fig. 11. These diverticula open into the depression by wide mouths.

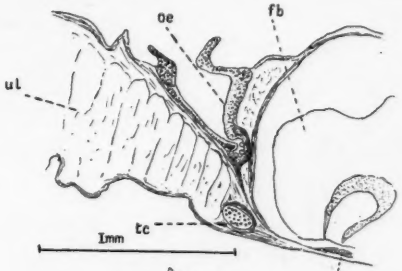

Fig. 10. 35 mm. embryo sagittal section, anterior end to the left. ×30.

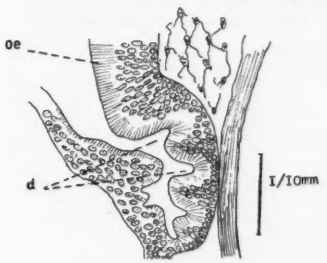

Fig. 11. 35 mm. embryo sagittal section. Enlarged view of primary diverticula. ×120.

The cells composing their walls are similar to those of the olfactory epithelium in other regions.

These diverticula are really paired being formed in two groups right and left of a median sagittal portion which extends forwards forming a kind of septum. This is shown in fig. 12 which is a horizontal section through an ammocoete larva of *Petromyzon fluviatilis* (*P. planeri* is similar). The cavity of the depression is V-shaped in this section owing to the paired nature of the groups of diverticula. This paired nature of the origin of this accessory organ is further evidence in favour of the secondary nature of monorhiny in cyclostomes.

The diverticula at this stage contain a substance which is highly refractive and which must be a product of secretion or excretion of the cells of the diverticula.

As development proceeds the diverticula become closed off and form vesicles,

and the cells lining them develop cilia. The vesicles sink in deeper beneath the surface (fig. 13) and at the same time extend laterally behind the olfactory

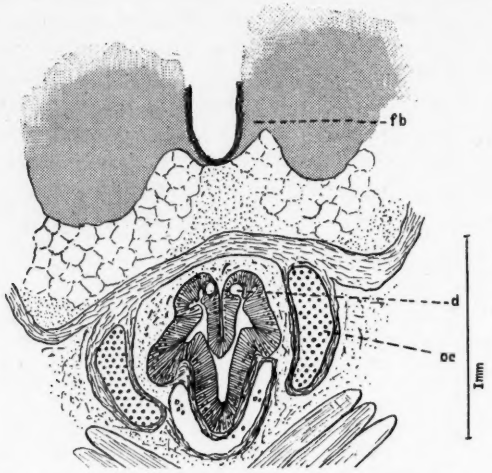

Fig. 12. Ammocoete of *P. fluviatilis*, horizontal section showing the paired nature of the origin of the prinary diverticula. ×30.

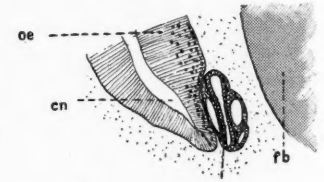

Fig. 14. Ammocoete sagittal section, lateral to Fig. 13. Anterior end to the left. ×30.

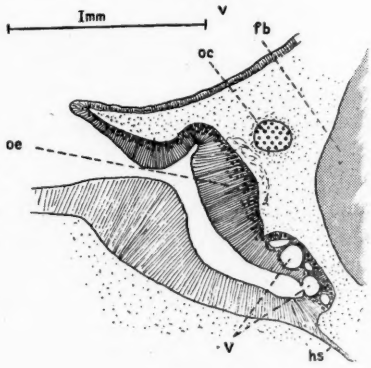

Fig. 13. Ammocoete sagittal section near the median plane, anterior end to the left. ×30.

epithelium and separated from it by limiting membranes (fig. 14). During metamorphosis the separation from the olfactory epithelium is complete and

the organ lies free in the olfactory capsule as two large masses of vesicles (figs. 1 and 4).

There remain to be accounted for the dorsal and lateral groups of vesicles in contact with the involutions of the olfactory epithelium. As already stated these arise by proliferation of cells in the epithelium (fig. 7). In the centre of the end of the involution a number of cells is seen which have lost the elongated form characteristic of the olfactory epithelium cells, and become spherical. These cells become larger as they are further removed from the epithelium and differentiate into the cells surrounding the vesicle which appears as a cavity in their midst.

The vesicles therefore have two modes of origin, one early from open diverticula which contain a secreted substance, the other later from cells proliferated by the epithelium and between which a lumen appears. In the adult the histological characters of both kinds are identical.

DISCUSSION

There is probably no fundamental difference between the two modes of origin of the organ. The fact that one part of it appears before the other is probably due to some function it performs in the larval period (cf. the secreted matter in the diverticula), and is sufficient to account for the difference in method of development. Cases of organs arising in instalments and with a certain amount of difference in the mode of origin are not rare. The Schneiderian folds of the olfactory invaginations in Selachians arise in two sets; the pronephric tubules precede the mesonephric and metanephric in appearance. That one set of vesicles should arise as open diverticula and the other as closed sacs is not significant. Many organs which are undoubtedly homologous may arise as hollow invaginations or as solid ingrowths in which a cavity later appears. Examples of this are to be found in the nerve-cord and the hypophysis. Besides, Lubosch (5) has observed one case in which a vesicle arose from an involution of the olfactory epithelium as a diverticulum, thus showing the continuity of the two processes.

With regard to the homologies of the organ Scott's claim that it represents Jacobson's organ must first be considered. Jacobson's organ in the higher chordates arises as paired diverticula from the olfactory sacs, which later lose connexion with the nose and acquire a communication with the mouth. Its precise function is doubtful but it is probably sensory. There is no recognised homologue of Jacobson's organ in the fish with the exception of the median diverticulum of the olfactory sacs in the Selachian (Sund (9)). When the process of development of Jacobson's organ is compared with that of the organ of Petromyzon there is little similarity. Jacobson's organ does not arise from the tips of the involutions of the olfactory epithelium and it consists of a pair of sacs, not a pair of groups of many vesicles. On the whole the evidence is not strong enough to warrant the assertion that the organ is

Jacobson's organ just because it is situated in the olfactory capsule and first arises as paired series of diverticula.

On the other hand the nose of higher chordates abounds in glands of various kinds (Bowman's, Steno's) and if the organ has a representative in higher forms, it is probably to be found in these.

With regard to the function of the organ in Petromyzon it has already been mentioned that previous investigators regarded it either as a gland, or merely as a rudimentary organ. But as some of them regarded the vesicles as communicating with the exterior by ducts, the fact that these ducts do not occur would probably modify their view. In my opinion the rudimentary nature of the organ can be dismissed, and its function must be either sensory or glandular.

In support of the view that it is sensory in function are the facts that it arises from the sensory epithelium of the nose, that its cells are ciliated and that it is innervated by branches which appear to be part of the olfactory nerve. But it is then difficult to account for the closed condition of the vesicles, and the fact that they are so closely surrounded by blood corpuscles.

On the other hand the presence of a substance in the first diverticula, of a coagulated fluid in the vesicles and of granules in the cells suggests a glandular function. That glandular cells may at the same time be ciliated is possibly not unknown in the animal kingdom. Prof. J. P. Hill, F.R.S., has very kindly informed me that the cells lining the epididymis have stereocilia and may be glandular. According to Jordan and Helvestine (11) the cells of the ductuli efferentes of the rat may possess vibratile cilia and begin to secrete, although later the cilia are lost. Saguchi (12) quotes Lenhossek, Frenzel and Tschassownikow as saying that in the pharynx of Amphibia cilia may co-exist with secretory activity, though he himself is doubtful. Cowdry (13) has shown that the follicle cells of the thyroid of some Elasmobranchs have flagella. Similarly Dustin (14) has described ciliated cells in the thymus, and Lams (15) in the oviduct of the rat. (See also Moreaux (16).) But if the vesicles are closed how is the secretion evacuated? This I believe to be the significance of the crowding of the blood corpuscles and therefore presence of blood round the vesicles. Since there is no communication between the vesicles (in the adult) and the exterior (although there was in the diverticula of the larva) the secretion must be carried away in the blood, and the organ be one of internal secretion. No other view will fit the facts; and although the proof of the endocrine nature of an organ is experimental, the evidence from morphology and embryology leads to the conclusion here enunciated as a hypothesis which it is hoped to be able to test by experimental methods.

Myxine and Bdellostoma were investigated in the hope of discovering something comparable to what has here been described for Petromyzon, but without any result.

Since the work described above was completed I have had occasion to test the action of the contents of the vesicles. An extract from 25 lampreys

(*P. fluviatilis*) was found to have no effect on the blood pressure of the cat, the melanophores of the frog or the capillaries of the same animals. These reactions are given by pituitary extracts, so that this negative result is additional evidence against the possibility that the organ may represent a part of the pituitary. It is not conclusive, however, for the only part of the pituitary which it could represent is the pars tuberalis, and the specific function of this part has not been determined in any animal. I desire to express my thanks to Dr Hogben of the Department of Physiology, Edinburgh, for assistance in this matter.

SUMMARY

1. The olfactory capsule of Petromyzon contains a vesicular organ; the vesicles are lined with ciliated glandular cells, they contain fluid, they are immersed in blood sinuses innervated by branches of the olfactory nerve, and are closed.

2. The vesicles arise in two sets:
   (i) from diverticula of the ventral portion of the olfactory epithelium in the young larva;
   (ii) by proliferation of cells from the ends of the involutions of the olfactory epithelium after metamorphosis.

3. The diverticula in the larva contain secreted (or excreted) matter.

4. The vesicles of the adult contain a fluid which must be evacuated through the blood.

5. There is insufficient evidence to indicate the homologies of the organ.

6. Nothing similar was found in any other form yet investigated.

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HYPERTROPHY OF THE PLATYSMA

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The *Platysma myoides* is a very variable muscle in the human species. Usually little developed, it may be more or less atrophied and even may not be found at all on dissection. This was the case on both sides of the dead body of a man, aged 20 years, who was dissected by some pupils of mine, on the 21st of January, 1924.

The Platysma may, on the contrary, have a more or less exaggerated development. I shall describe such a case, observed in a living subject, a medical student, E.M., 23 years old, on whom the subcutaneous muscles of the head and neck, especially the Platysma, are much hypertrophied.

Fig. 1 shows this subject, when he voluntarily contracts both his Platysmae. The buccal cleft then widens a great deal, the *Comissurae labiorum* sink and the genio-labial furrows become marked. One can note then the constitution of the Platysmae. A series of fasciculi of different thickness are distinguishable (six fasciculi are to be seen on the right side and eight on the left one, all of them in an oblique upward and inward direction). The most voluminous fasciculi are the most internal ones. When contracted, one notes between the latter a triangular fossa or excavation with its base below. This fossa is 2 cm. deep below the chin, being 3 cm. in width at this point and 7 cm. wide on a level with the interclavicular notch. When the Platysmae are contracted, one observes a slight transverse wrinkling of the skin.

This subject can at will contract the right Platysma or the left one separately as may be seen from Figs. 2 and 3. In these states, only the right commissura or the left one sinks, giving the physiognomy a truly strange appearance.

The skin of the thorax rises when those muscles are contracted and the nipple accompanies it in its ascent. The maximum displacement of the nipple is 8 mm.

As I have just said, all the subcutaneous muscles seem to be hypertrophied in this subject. He moves his scalp vigorously at will. His frontalis and occipitalis muscles are exaggerated in size and strength. He moves his ears at will, making them deviate as he moves them simultaneously upwards and a little backwards from which we infer an excessive development of the auricular muscles, especially of the upper one. He raises and lowers the alae nasi, deeply wrinkling the skin of the intersuperciliary region. When he does so, his physiognomy assumes the aggressive aspect shown in fig. 4.

Fig. 1. Voluntary contraction of both Platysmae.

Fig. 2. Voluntary contraction of right Platysma.

From photographs by Dr Pedro Vitorino.

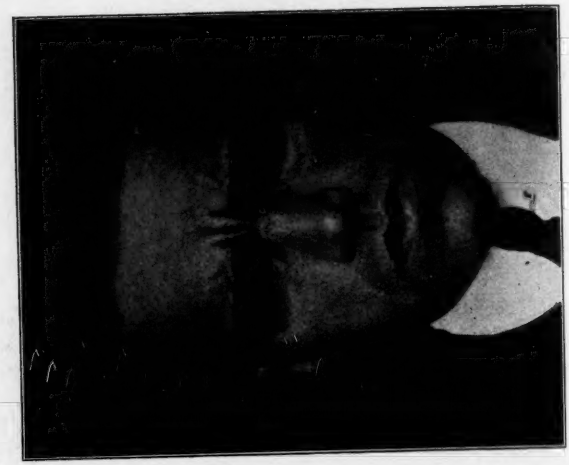

Fig. 4 Elevation of Alae nasi.

Fig. 3. Voluntary contraction of left Platysma.

This subject voluntarily provokes subluxations of both thumbs (fig. 5), as is also the case with his brother.

I have at other times remarked that the power of provoking subluxation of the thumb is sometimes familial. I am acquainted with two more families which possess this power: in one family there are a lady and three daughters, and in the other, mother and son.

Although possessing so many functional anomalies, this medical student is intelligent, and perfectly normal from a psychical point of view. It is curious to note that, being able to contract his subcutaneous muscles, voluntarily and so intensely, these do not seem to contribute to the expression of emotions more than in normal individuals.

Fig. 5. Voluntary subluxation of both thumbs.

Darwin (1) mentions a subject who could contract his Platysma on one side alone, and believed that this muscle, contrary to what Duchenne (2) taught, does not express terror and astonishment by itself, and that these emotions may even be manifested without the Platysma being contracted.

According to Wood, quoted by Darwin, the Platysma is more developed in subjects having a thin and long neck and broad shoulders. My case does not support this opinion. From the measurements I have taken, E.M. is a young man in whom the circumference of the neck and the breadth of the shoulders are in proportion to the stature:

Stature	1·66 m.
Circumference of neck on a level with upper border of the thyroid cartilage	0·36 m.
Biacromial breadth	0·41 m.

Beaunis and Bouchard (3) have seen a subject who voluntarily contracted the Platysma, either on one side alone or on both sides. Vigorous and simultaneous contraction gave the physiognomy, according to these authors, the aspect of a hanged man.

Testut (4) has noted the case of a hysterical girl whose Platysma was very much developed; when she contracted it, her mammary gland was strongly drawn upwards as in my case.

Lastly, Charpy (5) observed a subject who exhibited himself in public, and could throw his Platysma into contraction as intensely as indicated in Duchenne's photographs.

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LE *GYRUS TRANSVERSUS AREAE PIRIFORMIS* DU CERVEAU DES CARNASSIERS

PAR R. ANTHONY ET F. COUPIN

CHEZ les Canidés (Chien, Chacal, Renard), la scissure rhinale postérieure se prolonge très loin en arrière sur la face mésiale de l'hémisphère; le plus souvent, elle y atteint un sillon néopalléal perpendiculaire à sa direction et qui, sur nos figures 1 et 2, est désigné par les lettres *s.u.*

D'autre part, à une petite distance en arrière de l'extrémité antérieure de la fissure hippocampienne, et, partant de sa lèvre interne, on voit débuter une petite bande de substance grise qui a l'aspect d'un cordon aplati assez mal délimité de l'écorce de l'aire piriforme (*gyrus ambiens*). Cette bande de substance grise se dirige d'abord d'avant en arrière, puis de haut en bas,

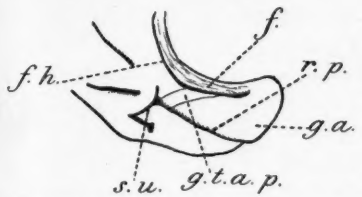

Fig. 1. Région de l'uncus, face mésiale, chez le Chacal (*Canis aureus* L.) ♀ No. 1920–74. (Ce numéro et les numéros analogues se rapportent aux réserves d'étude du service d'Anatomie comparée du Muséum national d'Histoire naturelle.)

f.h.=fissura hippocampi; *r.p.*=rhinale postérieure; *s.u.*=sulcus ursinus; *g.a.*=gyrus ambiens (area piriformis); *f.*=fornix (fimbria); *g.t.a.p.*=gyrus transversus areae piriformis.

Le gyrus dentatus est caché dans la fissure de l'hippocampe.

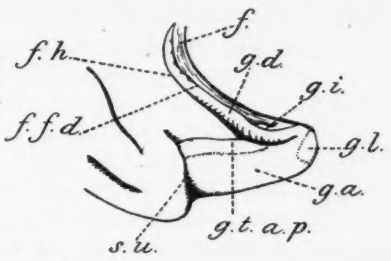

Fig. 2. Région de l'uncus, face mésiale, chez l'Ours brun (*Ursus arctos* L.) ♂ No. 1911–216.

g.d.=gyrus dentatus; *g.i.*=gyrus intermedius; *g.l.*=gyrus lunaris; *f.f.d.*=fissura fimbrio-dentata.

Pour la signification des autres lettres, voir la légende de la fig. 1.

suivant alors la courbure de l'aire piriforme de dedans en dehors, décrivant donc une légère courbe dont la concavité regarde en avant et en bas; cette bande s'élargit à mesure qu'elle se poursuit, en même temps que ses limites perdent de leur netteté, et s'achève immédiatement en avant du point où la scissure rhinale se jette dans le sillon *s.u.* (voir fig. 1). Cette petite circonvolution est mentionnée par G. Retzius[1] qui la désigne sous le nom de

[1] RETZIUS, G. "Zur aüsseren Morphologie des Riechhirns der Saügethiere und des Menschen." *Biol. Untersuch.* VII. 2–46, 1898.

Ibid. "Zur Morphologie der Fascia dentata und ihrer Umgebungen," *Biol. Untersuch.* VII. 3–5 (note), 1898.

gyrus transversus hippocampi. Ce nom ne lui convient pas; ce n'est pas en effet l'hippocampe qu'elle traverse, mais bien l'aire piriforme que beaucoup d'auteurs continuent encore de comprendre dans ce qu'ils appellent le *gyrus hippocampi* lequel est en réalité un composite fait de l'aire piriforme, partie du rhinencéphale et, plus haut, du *gyrus paradentatus*, partie du neopallium. Le nom qu'il faut donner à cette petite bande de substance grise est plus exactement celui de *gyrus transversus areae piriformis.*

Ce gyrus n'est nullement spécial aux Canidés, comme le pensait G. Retzius: on en constate la présence chez tous les Carnassiers lorsque sont réalisées certaines conditions que nous indiquerons plus loin. On le voit chez les Hyènes où la disposition des parties est très voisine de celle que nous venons de décrire. Chez les Ursidés (voir figs. 2 et 3), il est particulièrement net et bien accusé. Ici, la lèvre supérieure du sillon *s.u.* prend une extension considérable, operculisant quelquefois, comme c'est le cas de l'individu représenté fig. 2, l'extrémité de la rhinale postérieure qui s'arrête cependant alors avant d'en atteindre le fond. Le sillon *s.u.*, ou plutôt son ouverture a la face externe de l'écorce, est ce que l'on appelle chez les Ours le *sulcus ursinus.* Remarquons qu'en dépit de cette dénomination il n'est nullement spécial aux Ursidés: nous l'avons déjà vu exister chez les Canidés et les Hyaenidés, sous une forme atténuée il est vrai, puisque sa lèvre postérieure n'est pas à proprement parler operculisante, mais pourtant impossible à méconnaître. Le *gyrus transversus areae piriformis* suit, chez les Ursidés, à peu près le même trajet que chez les Canidés et les Hyaenidés: après avoir longé durant quelques millimètres la fissure hippocampienne, il s'en éloigne peu à peu, et, décrivant sous la lèvre operculisante du *sulcus ursinus* une courbe très fermée, à ouverture antéro-inférieure, qui coiffe l'extrémité de la rhinale (voir fig. 3), il va comme se perdre au fond du *sulcus ursinus* dans sa région la plus inférieure; tant qu'il suit le bord externe de la fissure de l'hippocampe, il est étroit et d'un aspect quelque peu indécis; à partir du moment où il s'en écarte, on le voit au contraire prendre un aspect godronné, plus net sur son bord postérieur que sur son bord antérieur; dans sa partie operculisée par la lèvre postérieure du *sulcus ursinus*, il s'élargit encore mais dessine souvent une moindre saillie, l'aspect godronné faisant place à un aspect grenu dû à ce que sa surface est recouverte de nombreux petites tubercules.

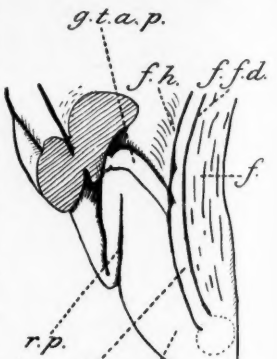

Fig. 3. Face supérieure de l'uncus chez l'Ours d'Amérique (*Euarctos americanus* Pall.) No. 1913–421; après excision de la lèvre postérieure operculisante du sulcus ursinus.

Pour la signification des lettres, voir les légendes des figs. 1 et 2.

L'apparence plus compliquée du *gyrus transversus areae piriformis* est ici due au grand volume cérébral lequel est en rapport avec la grande taille de

l'animal; on sait en effet que la complication de l'écorce, aussi bien rhinencéphalique que néopalléale, est toujours en rapport, si on la considère dans un groupe homogène, avec le volume du cerveau. Sa remarquable courbure à concavité antéro-inférieure, de même que l'extension de la lèvre postérieure du *sulcus ursinus*, est en rapport avec le recourbement de l'*uncus*, recourbement conditionné lui-même par l'augmentation du volume du cerveau et par le changement de forme particulier qui en est la conséquence.

Dans le cerveau du Chat domestique, on ne peut distinguer le *gyrus transversus areae piriformis*; mais, dans celui du Lion, il existe très nettement, présentant à peu près les mêmes caractères que ceux que l'on constate chez le Chien. Notons simplement qu'il paraît débuter plus loin de l'extrémité antérieure de la fissure hippocampienne, qu'il est particulièrement bien délimité en arrière, c'est à dire du côté de sa convexité, présentant dans cette région des godrons très nets, alors qu'en avant, c'est à dire sur son bord concave, il se confond presque insensiblement avec l'écorce de l'aire piriforme.

Chez le Coati (de la famille des Procyonidés), où la disposition des sillons est, dans la région qui nous occupe, à peu près la même que chez les Canidés, nous avons vu un *gyrus transversus areae piriformis* assez net mais qu'on ne distingue qu'à partir d'une certaine distance de l'extrémité antérieure de la fissure hippocampienne. Chez la Civette (de la famille des Viverridés), nous n'avons rien vu qui puisse lui correspondre.

Il paraît être également absent chez les Mustélidés bien que, cependant, chez la Loutre et la Fouine, on distingue, le long de la lèvre externe de la fissure hippocampienne, une crête atténuée qui se dirige vers l'extrémité de la rhinale postérieure et qui pourrait le représenter.

Chez l'Otarie que nous prenons ici comme représentant des Pinnipèdes, on rencontre une disposition rappelant de très près celle des Ours: le *sulcus ursinus* notamment a à peu près le même aspect, bien que nous n'ayons pas constaté que sa lèvre postérieure soit operculisante, au moins au même degré. Le *gyrus transversus* est très net.

En résumé, on observe le *gyrus transversus areae piriformis*, chez les Canidés, les Hyaenidés, les Ursidés, l'Otarie, les grands Félins, et, même, le Coati; on n'en voit point de trace chez le Chat et chez les Viverridés; il n'en existe que des indications, peu nettes en vérité, chez la Loutre et la Fouine. On doit donc le considérer comme une formation commune aux Carnassiers dont l'encéphale est assez volumineux et possède, par suite, une certaine complexité de plissements[1]. Remarquons d'ailleurs que les sillons du *gyrus ambiens* et beaucoup d'autres détails rhinencéphaliques ne sont, de même, visibles que chez les Carnassiers possédant de gros cerveaux.

Le *gyrus transversus areae piriformis* existe-t-il chez d'autres Mammifères? Ni chez les Ongulés, ni chez les Primates, ni chez les Cétacés, ni chez le Kanguroo, choisi, en raison de sa grande taille, comme type des Marsupiaux, nous ne l'avons rencontré.

[1] Le Chien que nous avons examiné pour cette étude était un Chien de grande taille.

Il représente évidemment une formation rhinencéphalique, puisque la partie de l'écorce sur laquelle il fait saillie est une dépendance du rhinencéphale, mais qui semble, si l'on s'en rapporte à ce que l'on voit, par exemple, chez les Ours, un pont jeté entre le rhinencéphale et le neopallium. Il est certain qu'il n'a rien de commun avec la bandelette de Giacomini de l'Homme et des Singes. Cette dernière n'est que la partie toute antérieure du *gyrus dentatus* replié sur lui-même en raison du recourbement exagéré (en quelque sorte et si l'on peut dire) de ce qu'on appelle en anatomie humaine le crochet hippocampien (*uncus*). S'il existait chez l'Homme un *gyrus transversus areae piriformis*, il ne pourrait être situé qu'en avant de la bandelette de Giacomini, dans la région où, sur la fig. 4, nous avons placé une croix.

Nous avons étudié la structure du *gyrus transversus areae piriformis* chez l'Ours blanc, le Chien et le Lion.

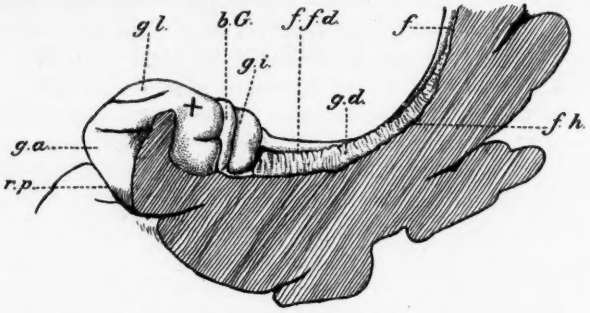

Fig. 4. Région de l'uncus, face mésiale, chez l'Homme. La lèvre interne de la fissure de l'hippocampe a été excisée pour montrer l'origine de la bandelette de Giacomini (*b.G.*). La croix (+) indique la place où devrait débuter, s'il existait chez l'Homme, le gyrus transversus areae piriformis.
Pour la signification des lettres, voir les légendes des figs. 1 et 2.

La fig. 5 représente une coupe coronale, c'est-à-dire parallèle au plan de la *lamina terminalis* et perpendiculaire à la fissure de l'hippocampe, de la région de l'*uncus*, chez un Ours blanc.

La *fissura hippocampi* (*F.h.*) divise le plan de cette coupe en deux parties: l'une, externe, qui correspond à l'hippocampe (*H.*) avec son *alveus* (*a.*) se prolongeant au delà du point α où cesse la structure hippocampienne caractéristique, au *gyrus dentatus* (*G.d.*) partiellement englobé du côté interne et vers le fond de la *fissura hippocampi* par une lame de substance dépendant de la couche la plus superficielle de l'hippocampe, au *gyrus intralimbicus* (hippocampe inverti) (*g.i.*) avec son *alveus* extra-ventriculaire, et, enfin, au *fornix* (*fimbria*) (*F.*); l'autre, interne, qui correspond à l'aire piriforme.

L'aire piriforme présente ici, comme partout, une structure moins spéciale que le *gyrus dentatus* et que l'hippocampe, se rapprochant davantage de celle de l'écorce néopalléale. On y distingue les couches suivantes se succédant de la superficie à la profondeur: une couche moléculaire (*m.*) assez épaisse con-

tenant à sa base un important plexus de fibres tangentielles (lame médullaire superficielle) (*l.m.s.*) sur lequel nous aurons à revenir; deux couches de cellules pyramidales (*P.* et *p.*) qui ne semblent guère, à la vérité, différer par la taille de leurs éléments, mais qui sont séparées par un espace plus clair (la couche

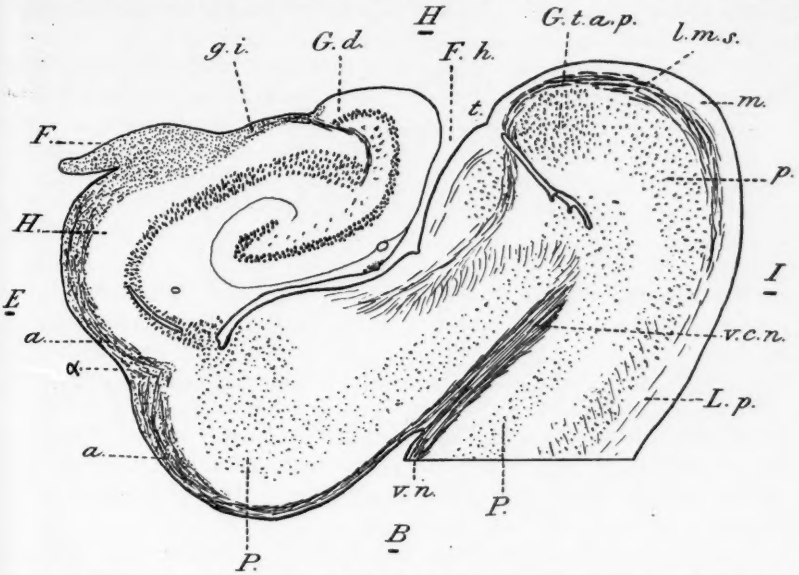

Fig. 5. Coupe coronale de la région de l'uncus chez l'Ours blanc (*Thalassarctos maritimus* Desm.) No. 1918–65.

Fixation au formol salé. Coloration suivant la méthode de Loyez.

F.h.=fissura hippocampi; *H.*=hippocampe avec sa couche de grosses cellules pyramidales et une partie de sa substance superficielle tendant à englober en dedans le gyrus dentatus; *G.d.*=gyrus dentatus avec sa couche de grains et, en dehors de cette couche, les cellules pyramidales non modifiées séparées de l'hippocampe par un faisceau de fibres se rendant au fornix, d'où il semblerait résulter que les axones, aussi bien de ces cellules pyramidales que des grains du gyrus dentatus, n'ont pas besoin de traverser la couche des cellules pyramidales de l'hippocampe pour se rendre au fornix; *F.*=fornix (fimbria); *g.i.*=gyrus intermedius (hippocampe inverti) recouvert d'une couche de fibres se rendant au fornix; *a.*=alveus; *v.c.n.*=voies conductrices néopalléales; *L.p.*=lobe piriforme; *m.*=couche moléculaire; *P.*=couche profonde des cellules pyramidales de l'aire piriforme; *p.*=couche superficielle des cellules pyramidales de l'aire piriforme; *l.m.s.*=plexus de fibres tangentielles de la couche moléculaire de l'aire piriforme (lame médullaire superficielle); *G.t.a.p.*=gyrus transversus areae piriformis; *t.*=sillon marquant la limite externe du gyrus transversus areae piriformis; *α*=point où la structure hippocampienne passe à celle du lobe piriforme; *H*=haut; *B*=bas; *E*=côté externe; *I*=côté interne.

la plus profonde (*P.*), et qui est la continuation de celle des cellules pyramidales de l'hippocampe, a nettement ici l'aspect radié qui lui a fait donner le nom de *stratum radiatum*); une couche de cellules polymorphes peu distinctes; vient enfin la substance blanche des voies conductrices.

Il est à noter que la région de l'aire piriforme qui borde la scissure de

l'hippocampe est très pauvre en cellules pyramidales. La couche superficielle de ces cellules n'y est pour ainsi dire pas représentée; sa place est occupée par un important faisceau de fibres blanches qui semble, pour une partie tout au moins, continuer la lame médullaire superficielle laquelle n'est plus que très réduite à ce niveau; cette formation paraît correspondre à ce qu'on appelle le *stratum lacunosum.*

Le *gyrus transversus areae piriformis* part d'un point *t.* situé au bord interne de la *fissura hippocampi* et marqué ici par une encoche; il se continue insensiblement avec l'aire piriforme. Au point de vue histologique il est peu différent de l'ensemble de cette dernière; sur cette coupe coronale ses seules particularités semblent être les suivantes: tout d'abord, les cellules pyramidales de la couche superficielle y sont beaucoup plus denses, plus nombreuses, que dans les autres régions, et plus rapprochées de la surface, la couche moléculaire présentant ici une moindre épaisseur; l'amas que constituent ces cellules pyramidales est séparé, en dehors, par un espace plus clair d'un autre amas de petites cellules qui, bien que dépassant du côté de la surface le faisceau de fibres blanches (continuation de la lame médullaire superficielle), peut-être considéré comme représentant la première couche des cellules pyramidales de l'aire piriforme dans la *fissura hippocampi.*

D'autre part, la lame médullaire superficielle, bien qu'amincie, paraît plus dense au niveau du *gyrus transversus* que partout ailleurs, ce qui semble bien être en rapport avec le plus grand nombre des cellules pyramidales de la première couche à ce niveau.

La fig. 6 représente une coupe oblique de l'aire piriforme chez le Lion; cette coupe croise à peu près à angle droit la direction du *gyrus transversus areae piriformis.*

On y voit les caractères essentiels déjà constatés chez l'Ours blanc: multiplicité des cellules pyramidales superficielles (*p.*) et minceur de la couche moléculaire (*m.*) au niveau du *gyrus transversus.* La lame médullaire superficielle (non représentée) est ici très réduite d'épaisseur.

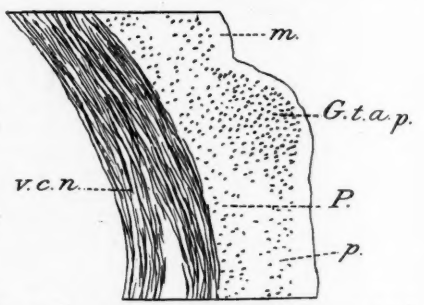

Fig. 6. Coupe oblique de la région de l'uncus chez le Lion (*Felis leo* L.) No. 1911–238. Fixation au formol salé. Coloration suivant la méthode de Loyez.

Pour la signification des lettres, voir la légende de la fig. 5.

La fig. 7 représente une coupe longitudinale du *gyrus transversus areae piriformis* chez le Chien. Elle est destinée à montrer les rapports que contractent les éléments de cette formation avec les fibres de l'*alveus* d'une part, et avec les voies conductrices néopalléales d'autre part.

En résumé, le *gyrus transversus areae piriformis* est une formation rhinencéphalique spéciale aux Carnassiers. Au point de vue histologique, il ne se

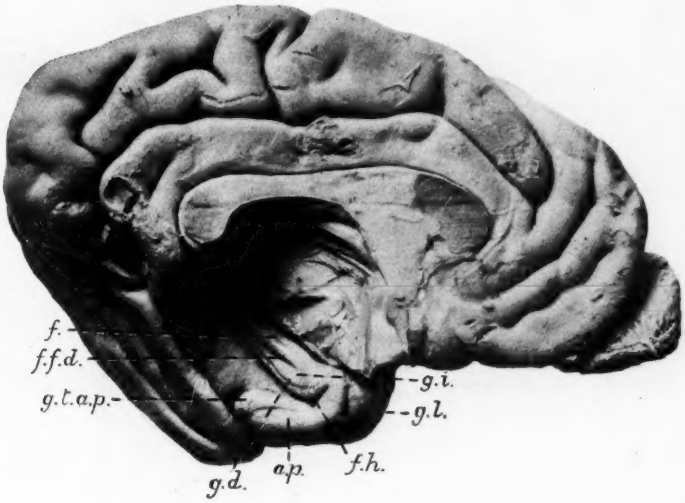

Fig. 1

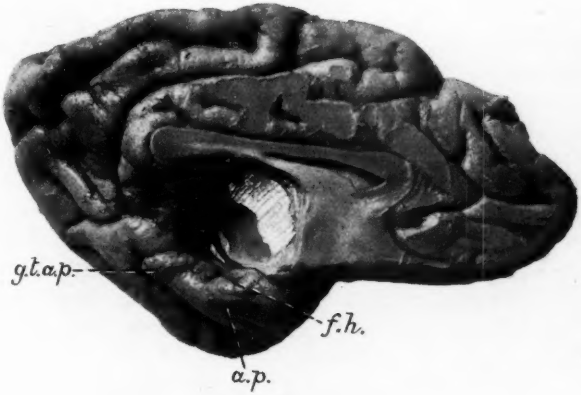

Fig. 2

distingue, chez l'Ours blanc et le Lion tout au moins, de l'*area piriformis* qu'il parcourt que par l'abondance des cellules pyramidales de la première couche et la réduction de la couche moléculaire à son niveau.

Il est hors de doute qu'il existe chez tous les Mammifères, par les communications entre les cellules du cortex piriforme et du cortex néopalléal avoisinant, une association des sens olfactif et gustatif, ce dernier paraissant bien devoir être localisé à la région du neopallium contiguë à l'aire piriforme.

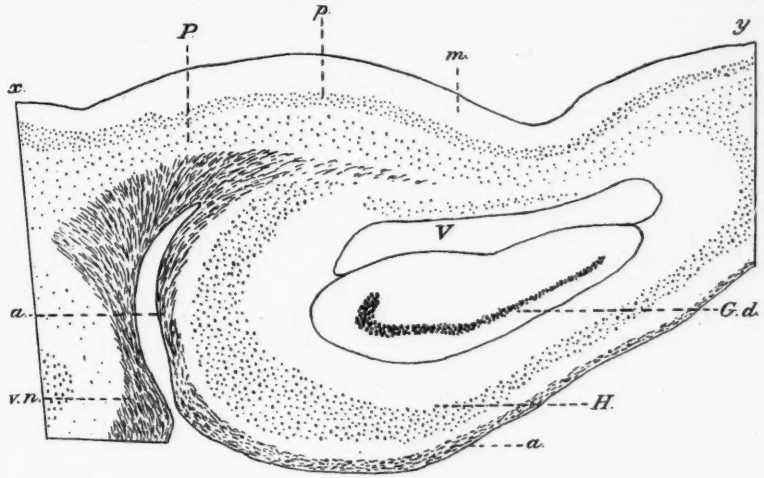

Fig. 7. Coupe longitudinale de *x* en *y* du gyrus transversus areae piriformis chez le Chien (No. 1914–31). Fixation au formol salé. Coloration suivant la méthode de Loyez.
V.=Diverticule de la cavité ventriculaire; *v.n.*=voies conductrices néopalléales. Pour la signification des autres lettres voir la légende de la fig. 5.

L'augmentation du nombre des cellules pyramidales, les axones des unes allant à l'*alveus*, et ceux des autres participant à la constitution des faisceaux conducteurs néopalléaux, suivant une bande de l'écorce qui va de l'extrémité antérieure de l'*uncus* au territoire néopalléal et qui constitue précisément le *gyrus transversus areae piriformis* est probablement en rapport avec le très grand rôle que doit jouer, au point de vue psychique, l'association des sens de l'odorat et du goût chez les Carnassiers.

LÉGENDE DE LA PLANCHE

Fig. 1. Hémisphère gauche (face mésiale) d'un Ours brun (*Ursus arctos* L.) ♀ No. 1921–15. G.N.
f.=fornix (fimbria).
f.f.d.=fissura fimbrio-dentata.
g.d.=gyrus dentatus.
a.p.=area piriformis.
f.h.=fissura hippocampi.
g.l.=gyrus lunaris.
g.i.=gyrus intermedius.
g.t.a.p.=gyrus transversus areae piriformis.

Fig. 2. Hémisphère gauche (face mésiale) d'un Lion (*Felis leo* L.) No. 1912–491. G.N.
Pour la signification des lettres voir la légende des figs. 1, 2.

THE FUNCTION OF THE SPINAL NUCLEUS OF THE TRIGEMINAL NERVE[1]

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More than twenty-five years ago Hun (10) published a very complete clinical record, including an account of the histological study of the brain stem made by Van Giesen, of a case of occlusion of the posterior inferior cerebellar artery. In the commentary it was stated "our case makes it certain that the fibres of the fifth nerve, after they have left the Gasserian ganglion, possess distinct functions, and that the fibres conveying impulses for thermic and painful perceptions are all collected together into the descending root of the fifth nerve; while all the fibres conveying impulses for tactile perceptions probably pass to the sensory trigeminal nucleus lying in the floor of the fourth ventricle."

Since the appearance of this important paper, several observers have suggested that the descending spinal root of the trigeminal nerve contains only fibres for the conduction of impulses concerned with pain and thermal impressions, and Spiller (14) has cited cases of obstruction of the posterior inferior cerebellar artery as offering conclusive proof of this contention. Nevertheless there still persists considerable hesitation in describing the spinal tract of the fifth nerve as solely composed of fibres concerned with the conduction of pain and thermal impulses, and this appears to be due chiefly to the variations in the distribution of the dissociated sensory loss which have been reported as consequent upon interference with the bulbar supply of the posterior inferior cerebellar artery. Our anatomical knowledge of the variation in distribution to the medulla of this vessel (17) explains the different forms of sensory loss found in a review of the reported cases of its occlusion, and the object of this paper is to study these cases in the light of recent anatomical research to see if convincing evidence about the function of the spinal root and nucleus of the trigeminal nerve cannot be deduced.

There is no doubt that occlusion of the posterior inferior cerebellar artery does offer a unique opportunity of studying the function of the spinal nucleus of the trigeminal, since its distribution (excluding that to the cerebellum) is invariably confined to the medulla and consequently this nucleus and its accompanying tract is the only part of the fifth nerve which can be affected.

[1] A portion of an investigation of sensation, for which a grant has been made by the Royal Society.

THE CENTRAL TERMINATION OF THE AFFERENT FIBRES OF THE TRIGEMINAL NERVE

The afferent fibres of the trigeminal nerve on entering the pons divide into two sets: a set of fibres which tend to ascend before they terminate in the main sensory nucleus situated in the tegmental part of the pons—and a second set of fibres which at once descend to form the well-defined spinal tract. On tracing this tract through the medulla to the first or second segments of the spinal cord, it is found to diminish gradually in size, owing to the regular termination of its constituent fibres in the spinal nucleus lying along its medial side. There appears to be ample evidence to prove that the sensory

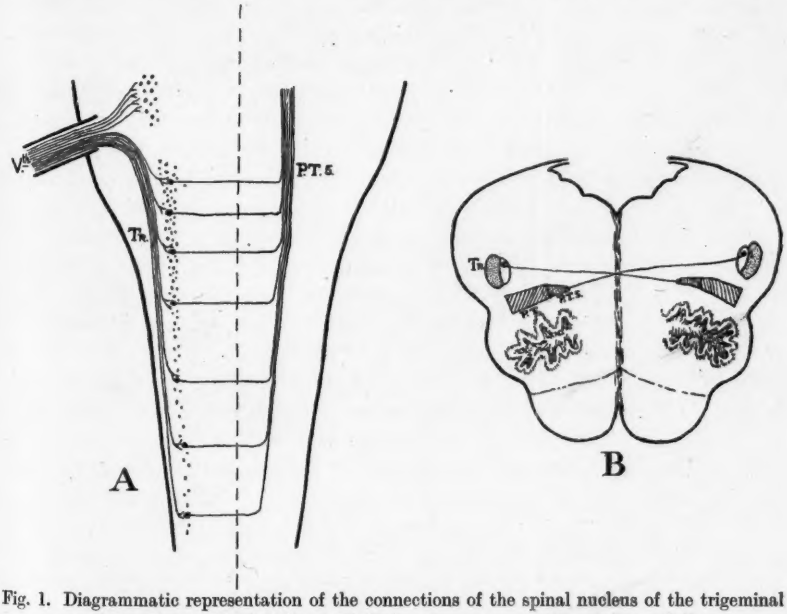

Fig. 1. Diagrammatic representation of the connections of the spinal nucleus of the trigeminal nerve: *A*, in a longitudinal section, and *B*, in a transverse section of the medulla.

Vth.	Sensory root of trigeminal nerve.
Tr.	Spinal tract and nucleus of trigeminal nerve.
P.T. 5.	Fibres arising from spinal nucleus and passing up to optic thalamus.
P.T.	Spino-thalamic tract.

fibres arising from the cells of the spinal nucleus cross the middle line and form a tract, in close relation to the spino-thalamic tract, in the retro-olivary region of the opposite side.

From a careful study of the clinical reports of patients suffering from occlusion of the posterior inferior cerebellar artery, there is evidence that these fibres, arising from the spinal nucleus, must cross the middle line almost transversely. The distribution of the dissociated sensory loss in the cases

referred to in a later part of this paper in Groups II and III would be unintelligible if these fibres crossed to any extent obliquely. It is of interest for later reference to notice that this tract lies in the deeper part of the substantia reticularis grisea (fig. 1 B), and from its position it appears likely that the small bulbar branches of the posterior inferior cerebellar artery may sometimes fail to reach it, although they supply the spino-thalamic tract.

THE POSTERIOR INFERIOR CEREBELLAR ARTERY

This vessel in about 70 per cent. of cases forms a loop on the lateral aspect of the medulla. The anterior and shorter limb ascends in relation with the postero-lateral sulcus, whilst the posterior and longer limb descends on the infero-lateral wall of the fourth ventricle before the artery turns laterally to supply the cerebellum. The length of the ascending limb is variable and this has an important influence upon the extent, especially in the cephalic direction, of the medulla supplied by the artery. Occasionally this loop is not present, the vessel passing almost directly outward to the cerebellum, in which form there are very few bulbar branches, or they may be absent altogether.

The ascending limb provides a number of fine branches which enter the medulla in the region of the postero-lateral sulcus, the number of branches being proportionate to the length of this limb; generally a few enter the restiform body from the descending limb, but not infrequently these are absent. The branches from the two limbs usually supply a considerable part of the formatio reticularis grisea and the restiform body, but the extent of the retro-olivary region supplied, particularly in a longitudinal direction, is subject to variation and dependent upon the number of bulbar branches. No branches are distributed to the substantia reticularis alba, in fact a somewhat variable amount of the deeper part of the substantia reticularis grisea remains uninjected. The extent of the medulla supplied is at its maximum in the mid-olivary region and decreases when traced in either a caudal or cephalic direction. The distribution has never been found, after special injection of the vessel, to extend in either direction beyond the limits of the inferior olive. In the majority, the vertical extent of its distribution is considerably less than that of the inferior olive, particularly in the cephalic direction.

The anatomical investigation of the variations in the bulbar distribution of the posterior inferior cerebellar artery have been confirmed by reports of the histological examinations of the brain stem after thrombosis of the vessel. Fig. 2 shows the variations in distribution in the mid-olivary region found after injection of the vessel, and the most important feature to notice for the purpose of the present paper is that the spinal nucleus and tract of the trigeminal nerve are generally supplied by the artery at this level, but may occasionally lie outside the injected area. The exclusion of the spinal nucleus and tract is only found when the bulbar branches of the artery are seriously

reduced in number, consequent upon a more irregular course, as when the vessel fails to form the characteristic loop. Sections at a higher level of the medulla frequently show the spinal nucleus and tract uninjected, so that it is quite clear on anatomical grounds that it is the cephalic extremity of the

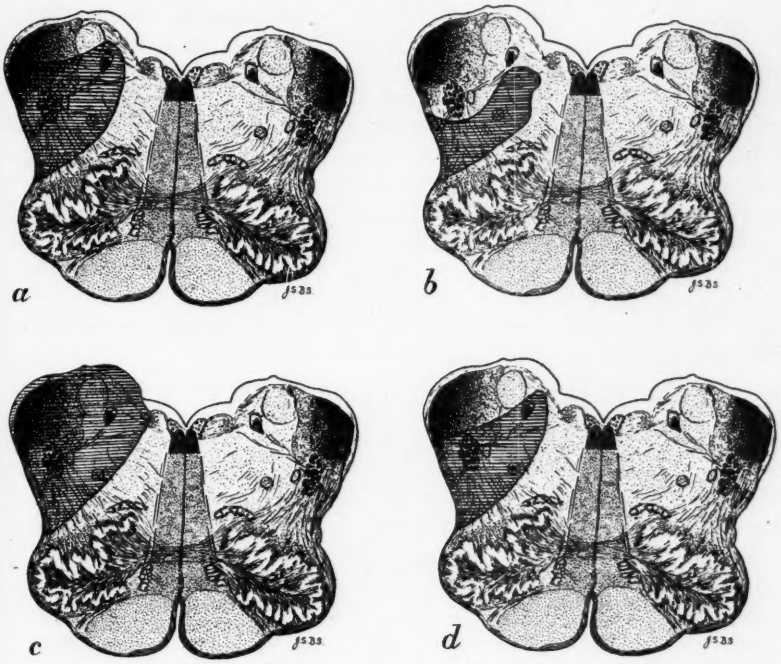

Fig. 2. Four variations in the distribution of the posterior inferior cerebellar artery at the mid-olivary level of the medulla.

spinal nucleus and tract which is most likely to escape after occlusion of the artery.

To avoid misunderstanding, it is necessary to mention that although the extreme caudal part of the nucleus does not receive branches from the posterior inferior cerebellar artery, the fibres in the spinal tract passing to this part are usually supplied in the olivary region and therefore are likely to degenerate after occlusion of the artery.

THE SENSORY LOSS FOUND AFTER OCCLUSION OF THE POSTERIOR INFERIOR CEREBELLAR ARTERY

It has been possible to procure reports of twenty-two cases of occlusion of this vessel in which there is an account of the distribution of the sensory loss and the elements of sensation affected. Several reports have had to be

excluded because no reference was made to the disturbance of sensation, and a few on account of complications induced by the presence of other nervous lesions which might render the interpretations fallacious. In a few of those under review, there was evidence that the thrombosis had extended to the vertebral, but these are presented because they offer valuable information and seem to be acceptable as reliable evidence, since we have very full knowledge of the distribution of this vessel to the brain stem.

In all the twenty-two cases, a dissociated loss of sensation was discovered, but the distribution of the analgesia and thermal anaesthesia was not constant and it is necessary to divide the cases into three groups. In Group I, consisting of no less than sixteen of the cases, the sensory loss was "crossed" and affected the face on the same side as the lesion, and the trunk and limbs on the opposite side. In four of these, the loss of sensation on the face was confined to a part or the whole of the distribution of the ophthalmic and superior maxillary divisions of the trigeminal nerve only, and in a fifth was limited to the ophthalmic division alone. Special reference later will be made to these five cases in which no sensory disturbance was found in the region supplied by the inferior maxillary division, since they shed considerable light upon the localisation of the termination of the three divisions of the nerve in the spinal nucleus.

Table to show source of clinical information quoted in text

Group I	Group II	Group III
Abrahamson, I. (1)	Bury, J. S. and Stopford, J. S. B. (3)	Gordinier, H. C. (6) (Case 3)
Gillis, A. C. (5) (Cases 1 and 2)	Courtney, J. W. (4)	Wilson, S. A. K. (20)
Hall, G. W. (7)	Gordinier, H. C. (6) (Case 2)	
Harris, W. (8) (Cases 1 and 2)	Müller, E. (12) (Case 2)	
Head, H. and Holmes, G. (9)		
Hun, H. (10)		
Mai, E. (11)		
Müller, E. (12) (Case 1)		
Ramsbottom, A. and Stopford, J. S. B. (13)		
Starr, M. A. (15)		
Stewart, R. M. (16)		
Thomas, H. M. (18) (Cases 1 and 2)		
Wallenberg, A. (19)		
Total 16	Total 4	Total 2

In two out of the sixteen in Group I, tactile sensation is mentioned as being slightly affected in the face on the side of the lesion. In Hall's report, it is quite evident that the lesion extended into the pons, since there was paresis of the facial muscles, and it seems likely that the thrombosis had spread into the upper part of the vertebral artery. Extension of the lesion into the pons is likely to affect fibres of the trigeminal nerve other than those which pass into the spinal root, and this may account for the slight defect in tactile sensation recorded by Hall. In the other, which was reported by Müller (case 1), there is also evidence which suggests that the clot had extended into the vertebral, and consequently it is possible that the pontine nucleus was involved.

In Group II, composed of four cases, we find analgesia and thermal anaesthesia affecting the face, trunk and limbs on the side opposite to the lesion. In one of these, the dissociated sensory loss was confined to the ophthalmic division of the nerve only, but in the other three was found in the whole field of distribution of the trigeminal. In none was any loss of sensation discovered on the same side of the face as the lesion, although Gordinier refers to pain being experienced in that position, and it is probable that irritation of the spinal nucleus and tract by the neighbouring focus of degeneration was responsible for the pain.

In Group III we place two cases in which a dissociated sensory loss was found on both sides of the face and on the limbs and trunk of the side opposite to the lesion.

In Group I it is clear that the occlusion of the artery must have interfered with conduction in the spinal tract of the fifth nerve and the spino-thalamic tract, both of which are generally found in that part of the retro-olivary region to which branches are distributed.

In Group II, the anatomical explanation of the distribution of analgesia and thermal anaesthesia is less readily recognised. Interruption of the spino-thalamic tract must account for the loss of sensation in the opposite limbs and half of the trunk, as in the preceding group. The absence of sensory loss on the same side of the face as the lesion indicates that in the cases assigned to this group, the spinal nucleus and tract of the fifth nerve were not supplied by the artery, a condition which was found to exist occasionally by injection of the vessel. The disturbance of sensation in the half of the face opposite to the lesion must be the result of implication of the fibres arising from the opposite spinal nucleus as they lie in the deeper part of the substantia reticularis grisea. From my injections of the posterior inferior cerebellar artery, it is possible to state that such a distribution of the vessel is found.

In Group III, it is evident that not only are the spino-thalamic tract and the spinal tract of the trigeminal on the side of the lesion affected, but in addition, the fibres arising from the opposite spinal nucleus, after they have crossed the middle line—a form of distribution not so uncommonly seen as the small number of cases in Group III would suggest.

Since the sensory disturbance found in all the twenty-two cases, excluding the two in which there seems to be strong evidence for the view that the clot had extended into the vertebral artery, was an analgesia and thermal anaesthesia without any tactile anaesthesia, there appears to be no doubt that the spinal tract of the trigeminal contains only those sensory fibres concerned with the conduction of impulses induced by painful and thermal stimuli. The fibres concerned with the other elements of sensation must terminate in the sensory nucleus in the pons, and for this reason Hall's case, in which facial paralysis was associated with some interference of tactile sensation, is of particular interest. In neurological literature, a number of cases exhibiting tactile anaesthesia of the face consequent upon a pontine lesion may be found,

but it has not been considered necessary to review them in this paper, since the evidence with regard to the fibres passing to the spinal nucleus appears to be so definite.

THE TERMINATION OF THE THREE DIVISIONS OF THE TRIGEMINAL NERVE IN THE SPINAL NUCLEUS

Two chief opinions have been expressed about the arrangement of the termination of fibres from different parts of the face in the spinal nucleus.

First, there is the theory advanced, solely on clinical grounds, that there is a segmental arrangement similar to that found in the case of the spinal nerves. Woods (21) maintains that the caudal part of the spinal nucleus receives pain and temperature fibres from the strip of skin marked *A* in fig. 3, and that higher portions of the nucleus receive fibres successively from the strips *B*, *C*, *D* and *E*: thus fibres from the region around the mouth pass to the most cephalic part of the nucleus. The clinical evidence upon which this suggestion is based is unfortunately unreliable. Woods builds his hypothesis upon two cases: in the first, the irregularity of the syringomyelic cavities renders it unsuitable for the purposes of localisation, and in the second, the absence of a post-mortem examination makes it worthless.

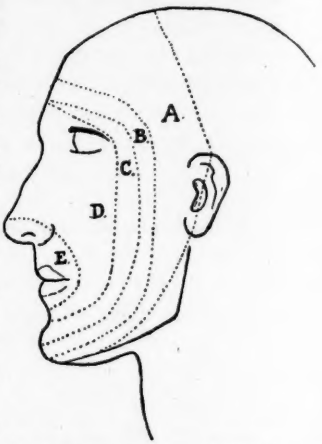

Fig. 3. To illustrate Woods' (21) theory with regard to the termination of the three divisions of the trigeminal nerve in the spinal nucleus.

Secondly, both clinical and experimental evidence has been advanced to show that pain and thermal fibres from the ophthalmic division descend to the caudal part of the spinal nucleus, whilst those from the maxillary division reach the intermediate part, and those from the mandibular division terminate in the cephalic portion. Here again the clinical evidence hitherto submitted fails to be convincing. Spiller (14) supports this view by quoting two cases of syringomyelia, in neither of which is any autopsy reported, and in both it had to be presumed that the spinal nucleus was affected. Since we know so accurately the distribution of the posterior inferior cerebellar artery, cases of occlusion of this vessel may be used with confidence in deciding this matter. In the twenty-two cases previously referred to, attention has been drawn to the fact that in Group I, in five out of the sixteen cases, it was reported that the dissociated sensory loss on the face was confined to the ophthalmic and maxillary branches, there being no sensory disturbance in the distribution of the inferior maxillary division. In one of the four cases in Group II, the sensory loss only affected the ophthalmic area. In six out of twenty-two cases, it is found that there was no sensory loss in the distribution of the inferior

maxillary division, and it seems probable that this is a low proportion, since the fact would only be noted if the extent of analgesia and thermal anaesthesia was mapped out carefully, as it can be very easily missed in an ordinary routine clinical examination. In none of the twenty-two cases was the region supplied by the ophthalmic division unaffected, and in only two did the superior maxillary area escape. These facts about the peripheral distribution of the sensory disturbance as a result of a central lesion, are of considerable significance and importance when it is remembered that injections of the posterior inferior cerebellar artery have demonstrated that it is the cephalic extremity of the spinal tract and nucleus which is most likely to escape, after occlusion of the vessel. There is strong anatomical and clinical evidence in support of the view that the most cephalic part of spinal nucleus of the trigeminal receives fibres from the inferior maxillary division, and it appears highly probable that the intermediate part is connected with the superior maxillary division, whilst the ophthalmic division terminates in the caudal part.

The experimental work of Bochenek (2) and others not only supports this contention, but supplies information about the position of the fibres of the various divisions of the trigeminal in the spinal tract.

The combined evidence from all sources seems to show conclusively that the central arrangement of the three divisions of the trigeminal nerve is just the reverse of the peripheral.

CONCLUSIONS

1. Cases of occlusion of the posterior inferior cerebellar artery offer unique opportunities for studying the function of the spinal nucleus of the trigeminal nerve, and the arrangement of the fibres in the spinal tract.

2. There appears to be no doubt that only those sensory fibres concerned with the conduction of impulses induced by painful and thermal stimuli, terminate in the spinal nucleus. Fibres concerned with the other elements of sensation must pass to the sensory nucleus in the pons.

3. Anatomical, clinical and experimental evidence seems to show conclusively that the fibres of the ophthalmic division descend to the caudal part of the spinal nucleus; those of the inferior maxillary division terminate in the cephalic division, whilst the fibres of the superior maxillary division end in the intermediate part of the nucleus.

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ADDENDUM

Since completing this paper my attention has been drawn to a contribution by Margaret W. Gerard (*Archives of Neurology and Psychiatry*, March 1923, p. 306), in which similar conclusions are reached and which includes important experimental evidence.

THE MAIN PERIPHERAL CONNECTIONS OF THE HUMAN SYMPATHETIC NERVOUS SYSTEM

By T. K. POTTS, M.B., Ch.M. (Sydney)[1]

The recent investigation (5, 7) of the functional significance of the sympathetic system by Dr N. D. Royle and Professor J. I. Hunter has revealed the necessity for a re-examination of the anatomy of the human sympathetic system. In particular the operations of ramisection (7, 8) devised by Dr Royle, in collaboration with Professor Hunter, call for a more exact determination of the precise position and topographical relations of the sympathetic cord and its *rami communicantes* than at present is available. The dissection described in this note was undertaken primarily to provide the surgeon with this guidance.

In this matter, two regions stand out as having assumed an added interest in the light of recent research. I refer to those regions associated with the operations known as cervical, and lumbar sympathetic ramisection, which are performed to remove the rigidity of the musculature of the extremities in spastic paralysis (2, 3, 4, 5, 7, 8, 9, 10).

As a description of the *rami communicantes* necessarily involves some mention of the arrangement of corresponding ganglia, this will be done in considering the various regions. To facilitate demonstration, the services of Miss D. Harrison were procured and, under my guidance, faithful reproductions of the dissection were made by her. The dissection has been mounted, and placed in the Wilson Museum of Anatomy, at the Medical School, University of Sydney.

The cervical portion of the sympathetic is characterised by the absence of segmental ganglia, and of white *rami communicantes*. Two constant ganglia are found—the superior and inferior cervical ganglia—and a variable middle cervical ganglion, variable in that it may be absent; and, when present in its usual position, lying commonly about the level of the inferior thyroid artery, i.e. the level of the 6th cervical vertebra; or else lying in close proximity to the inferior cervical ganglion. When this latter arrangement is found, the two ganglia are commonly united by stout cords embracing the vertebral artery. The absence, or the position when present, of this middle ganglion, affects the arrangement of the grey rami to the 5th and 6th; or 4th, 5th, 6th and 7th cervical nerves.

The superior cervical ganglion is usually placed at the level of the 2nd and 3rd cervical vertebrae, and under cover of the posterior belly of the digastric muscle, or a little above that level. This ganglion furnishes grey rami to the 1st, 2nd and 3rd, and, sometimes also, the 4th cervical nerves; in this specimen,

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to the 1st, 2nd and 3rd only. The 1st cervical nerve is not shown in the diagram (vide Pls. 1 and 6). These rami lie in the region of the lateral border of the longus capitis muscle, and join the nerve, as a rule, as it lies in the groove of the transverse process of the vertebra, or as it emerges from the groove between the anterior and posterior tubercles of the transverse processes. Furthermore, the ramus joins the nerve on the anterior, or antero-inferior aspect of the nerve. I have not seen an instance of a ramus junctioning with a spinal nerve on the posterior aspect of the latter.

The middle cervical ganglion, when situated about the level of the 6th cervical vertebra, usually supplies rami to the 5th and 6th cervical nerves; at times, also, to the 4th and 7th. When this ganglion is absent, or lies in close proximity to the inferior cervical ganglion, these cervical nerves, the 5th and 6th, and possibly also the 4th and 7th, usually derive their rami direct from the sympathetic trunk (Pl. 1); and it is my experience that this middle ganglion, when lying adjacent to the inferior ganglion, plays a subsidiary rôle from the point of view of furnishing rami to the cervical nerves. In this specimen only one ramus, viz. one to the 8th nerve on the right side, arose from this ganglion; but the ganglion contributes largely to the cardiac plexuses —especially on the left side (Pl. 1).

Here I would draw attention to two rami (Pl. 1) arising from the sympathetic trunk about the level of the anterior tubercle of the transverse process of the 6th cervical vertebra. They run a more or less parallel course, cranially and medially, pierce the longus colli muscle, and then pass directly backwards in the interval between the transverse processes of two adjacent vertebrae; and, in this case, the upper ramus is associated with the 5th cervical nerve, and the lower with the 6th. Both these rami effect junction with the nerves as the latter lie in the grooves of the transverse processes of corresponding vertebrae. At first I thought these rami were muscular twigs to the longus colli muscle; but subsequent dissection revealed the facts as stated. In addition, both rami give twigs to the vertebral artery.

The inferior cervical ganglion is commonly situated in the region of the level of the neck of the first rib, but may occupy a slightly lower level. The ganglion supplies rami to the 7th and 8th cervical, and 1st thoracic nerves (Pls. 2 and 7). A single ganglion may supply two or more spinal nerves, or two ganglia may supply a single spinal nerve; and here is an excellent illustration of the former. A ramus ascends in front of a spinal nerve, or nerves, if that ramus is associated with a nerve at a higher level. For example, it passes in front of the 8th and 7th if ascending to the 6th cervical nerve, and does not pass behind the nerve or nerves. A ramus in this region measures, as a rule, from ·5 mm. to 1·5 mm. across.

The scalenus anterior muscle presents an important relation to the grey rami in this region. The 5th and 6th or 7th nerves may lie in front of this muscle, may pierce the muscle, or may lie under cover of the muscle. So that in some cases in which these nerves lie upon, or pierce this muscle, it is not

uncommon to find all the rami, or some of them, lying upon the surface of the muscle, or wandering among its fibres. In the supposedly normal type, when these cervical nerves lie behind the muscle, the rami may lie upon, or pierce the muscle.

The inferior cervical ganglion is here shown as supplying one grey ramus to the 6th cervical nerve, two to the 7th, three to the 8th, and one to the 1st thoracic nerve, i.e. seven. There are still others requiring mention. I wish to draw attention to two or three rami on this specimen which lie to the medial side of the vertebral artery in a triangle formed by the upper border of the neck of the first rib below, by the lateral margin of the longus colli muscle medially, and by the medial border of the vertebral artery laterally. The shorter and more medially placed is a large ramus (which may be double) lying almost under cover of the lateral border of the longus colli muscle (Pls. 1, 2 and 7). It joins the 8th cervical nerve under cover of the muscle. The other ramus, single on the left side, double on the right, lies to the outer side of the last-mentioned ramus; and, taking the medial border of the vertebral artery as its guide, ascends upwards, and medially. This ramus appears to be fairly constant. It was present in the same position as a single trunk on the left side, and as a double trunk on the right in this specimen; and as a single trunk it was present on both sides of a full-term foetus; and also in a dissection of another adult cadaver. On only one occasion was it a double trunk. In every instance its main association is with the 7th cervical nerve; the greater proportion of its fibres turning distally at its point of junction with the nerve, while the nerve lies in the groove between the 6th and 7th cervical vertebrae. A fine branch is also continued upwards to the 6th cervical nerve; and in one case was followed on to the 5th nerve. At first I regarded this ramus as the vertebral plexus, aggregated into a single or double trunk at its commencement; but subsequent dissection has convinced me that it is a grey ramus associated mainly with the 7th cervical nerve.

To summarise, then, I have found three rami to the 5th cervical nerve; three to the 6th; three to the 7th, and three to the 8th; so these cervical nerves, 5th, 6th, 7th and 8th, may derive their rami from three sources, viz. from the sympathetic trunk; from the middle cervical ganglion (whatever its position when present); from the inferior cervical ganglion. In addition to these, Spalteholz(11) mentions branches from the vertebral plexus to these cervical nerves. The first white ramus, which is associated with the 1st thoracic nerve, connects this nerve to the inferior cervical ganglion, or to the 1st or 2nd thoracic ganglion. This white ramus is larger and whiter than the corresponding grey ramus, and lies lateral to, or lateral and posterior to the grey ramus, and is directed from above downwards and medially (Pls. 6 and 7). This white ramus must be left intact in the operation of cervical ramisection if pupillary effects are to be avoided.

The thoracic region is characterised by the segmental arrangement of ganglia; and, further, by the fact that there is at least one white and one

grey ramus associated with each thoracic nerve (Pls. 3 and 6). These white rami, together with those of the 1st and 2nd, or 3rd lumbar nerves, constitute the thoraco-lumbar outflow; which is restricted to that portion of the cord which lies between the cervical and lumbar enlargements. These latter, to quote Langdon Brown (6), "are devoted to the innervation of somatic muscles of the limbs. So much have these areas become specialised for this purpose, that the limbs have to obtain their visceral fibres from the part of the cord which lies between them."

In the thoracic segments the white ramus is more caudally placed than the accompanying grey ramus. Here again coalescence or fusion of neighbouring ganglia will somewhat affect the point of attachment of rami to the ganglia or sympathetic trunk. The general direction of the white rami in the thorax is from above, downwards, forwards and medially; and of the grey, upwards, backwards and laterally, with the exception of those grey rami of the 11th and 12th nerves, which are seen to descend from above, downwards, backwards and laterally. Here I may mention some of the common methods of junction of rami with ganglia or cord on the one hand, and with spinal thoracic nerves on the other (Pls. 3 and 6). There is a single ramus to the 2nd thoracic nerve. This is probably a mixed white and grey ramus. A simple arrangement is seen in the case of the 1st and 3rd nerves in which each ramus effects junction independently with both ganglion and spinal nerves. In the case of the 4th and 5th nerves, the two rami are fused at the point of junction with the nerves, and each ramus joins the corresponding ganglion independently. The reverse of this may occur, as in the case of the 9th nerve—the rami arise independently from that nerve, and coalesce before joining the corresponding ganglion. The 7th, 8th and 10th nerves have three separate communications, and more or less complete fusion of these occurs before connection with the ganglia, or as occurs in the case of the 7th nerve, with the sympathetic trunk. The reverse of this is seen at the 11th and 12th nerves; except that, at the 12th, there are four rami instead of three, as at the 11th. It will be noticed also that the rami tend to increase in length; and the number of rami to each nerve to increase as we proceed towards the abdomen. The increase in length is due to the forward inclination of the sympathetic trunk as it approaches the lumbar region. From the 9th, 10th, and 11th and 12th nerves, some branches to the intercostal muscles are given off, which at the 10th, and to a lesser degree at the 9th, are closely associated with the rami. The most caudal ramus of the 12th nerve joins the sympathetic trunk behind the renal artery. The next ramus above joins the nerve to the last thoracic ganglion; and the two ascending rami join the nerve to the last ganglion but one, thus affording an illustration of two ganglia supplying a single nerve.

The abdominal part of the sympathetic trunk (Pls. 4, 6 and 8) lies upon the bodies of the vertebrae, along the medial border of the psoas major muscle; and on the right side it is under cover of the inferior vena cava, and usually in front of the lumbar vessels; but also may lie behind. On the left side the

trunk usually lies in front of the vessels. The number of ganglia in the lumbar regions is very variable. "The ganglia are small; commonly four are, but a smaller number may be present. There are usually two connecting branches to each ganglion (12)." Harman (1) states that "the segmental arrangement of ganglia is the exception in this region, numbering up to eight"; and further states that "the numerical arrangement of the rami was even more variant, four rami to a ganglion being common." He also reports the double nature of the cord in this region. This condition existed on both sides in this specimen. Harman also states that "there is a marked and sudden change in the character in the constituents of the rami in connection with the 2nd and 3rd lumbar nerves. The rami of the 2nd nerve contain many fine medullated fibres, and which are arranged in characteristic bundles which number on an average over two hundred fibres, whilst the ramus of the 3rd nerve contains but few medullated fibres; and these are of quite a different character, and scattered at intervals throughout the mass of the non-medullated fibres in a manner which distinguishes them from the typical bundles of small, white, efferent fibres of a white ramus. The presence of a few scattered white fibres in a ramus otherwise grey does not constitute that ramus a white ramus." The rami pass under cover of the fibrous arches which give origin to fibres of the psoas major muscle; but in some instances may traverse the fleshy origin of this muscle; and in Quain's *Anatomy* it is stated (12) that "the rami may pass superficial to these fibrous arches."

Four ganglia are present in this specimen on both sides. The uppermost is a large ganglion lying upon the lower half of the body of the 2nd lumbar vertebra, the inter-vertebral disc, and the upper half of the body of the 3rd lumbar vertebrae. The 2nd and 3rd ganglia are almost fused, a slight constriction differentiating them. From this level to the 4th lumbar ganglion the cord is double, although on the left side the posterior division may be regarded as a ramus to the 5th lumbar nerve, communicating by a fine thread with the 4th lumbar ganglion. On the right side, the two divisions reunite, and are continued downwards as the main-trunk. The rami of the five lumbar nerves number two in each case. An elongated grey ramus descends from the last thoracic ganglion to the first lumbar nerve. From this nerve a large white ramus descends downwards, forwards and medially to join the uppermost lumbar ganglion in this case, or the 2nd ganglion when that exists independently. This is a very constant ramus, and can be readily avoided in lumbar ramisection. Some of its fibres are ultimately distributed to the bladder and rectum by way of the hypogastric nerves. The rami of the 2nd lumbar nerve pursue an arched course from the ganglion, upwards and backwards, and then turn abruptly downwards and backwards to join the nerve. The rami of the 3rd lumbar nerve proceed from the lower end of the uppermost ganglion down wards and backwards. Neither the 2nd or 3rd ganglion furnishes any rami directly in this case; the rami of the 4th lumbar nerve arise from the constriction between the two ganglia by a single trunk, and they are united before

entering the nerve by a fine cross-branch. One ramus to the 5th nerve arises directly from the 4th lumbar ganglion. The other ramus is really the continuation of the larger and posterior division of the sympathetic trunk, which receives a fine communication from the 4th lumbar ganglion, as already stated. One feature of the rami of this region is that they lie in the grooves of the bodies of the corresponding vertebrae; and in general are not in contact with the prominences of the intervertebral discs.

In the sacral region (Pls. 5 and 6) the sympathetic trunk is well defined; and again shows evidence of division into two strands as between the 2nd and 3rd sacral nerves of both sides, or even into three strands, as between the 3rd and 4th nerves on the left side. The ganglia in this region are very definite, are rounded, about the size of a pea, or smaller, and number four on the left side, and five on the right. The upper one or two are situated well above the corresponding nerves; but the lower two or three lie on the same level, and in close proximity to the nerves. The largest ganglion of this series is the uppermost on the right side; and in addition to supplying four rami to the 1st sacral nerve, it communicates with the 2nd sacral nerve by a large ramus, which has a definite ganglion at its junction with the nerve. This ramus also has a cross-branch connecting it with the sympathetic trunk. The 4th sacral ganglion on the left side is joined by a ramus to the ganglion of the 3rd nerve of the right side, and by a second ramus to a branch from the ganglion of the 4th sacral nerve of the right side. The rami vary greatly in number; from one or two to a single nerve, up to eleven, as in the case of the 4th ganglion of the left side. On both sides there is a rich supply of rami associated with the 1st sacral nerve. On the right side, four large individual rami; and on the left, two, one of which is as large as to suggest fusion of two or more rami. Rami to the 2nd and 3rd sacral nerves pierce the pyriformis muscle. A portion of this muscle has been removed on the right side. From the ganglion of the 4th nerves of both sides, and also from that of the 3rd nerve of the right side, branches are given off to the pelvic plexuses. One branch from the ganglion of the 4th nerve of the left side communicates with the pudendal nerve of the same side. The sacral visceral nerves, or the pelvic splanchnic nerves of Gaskell, which constitute the sacral portion of the parasympathetic nervous system arise as usually described, from the 2nd and 3rd spinal nerves.

I wish to express my gratitude to Professor Hunter for advice and information willingly given at all times.

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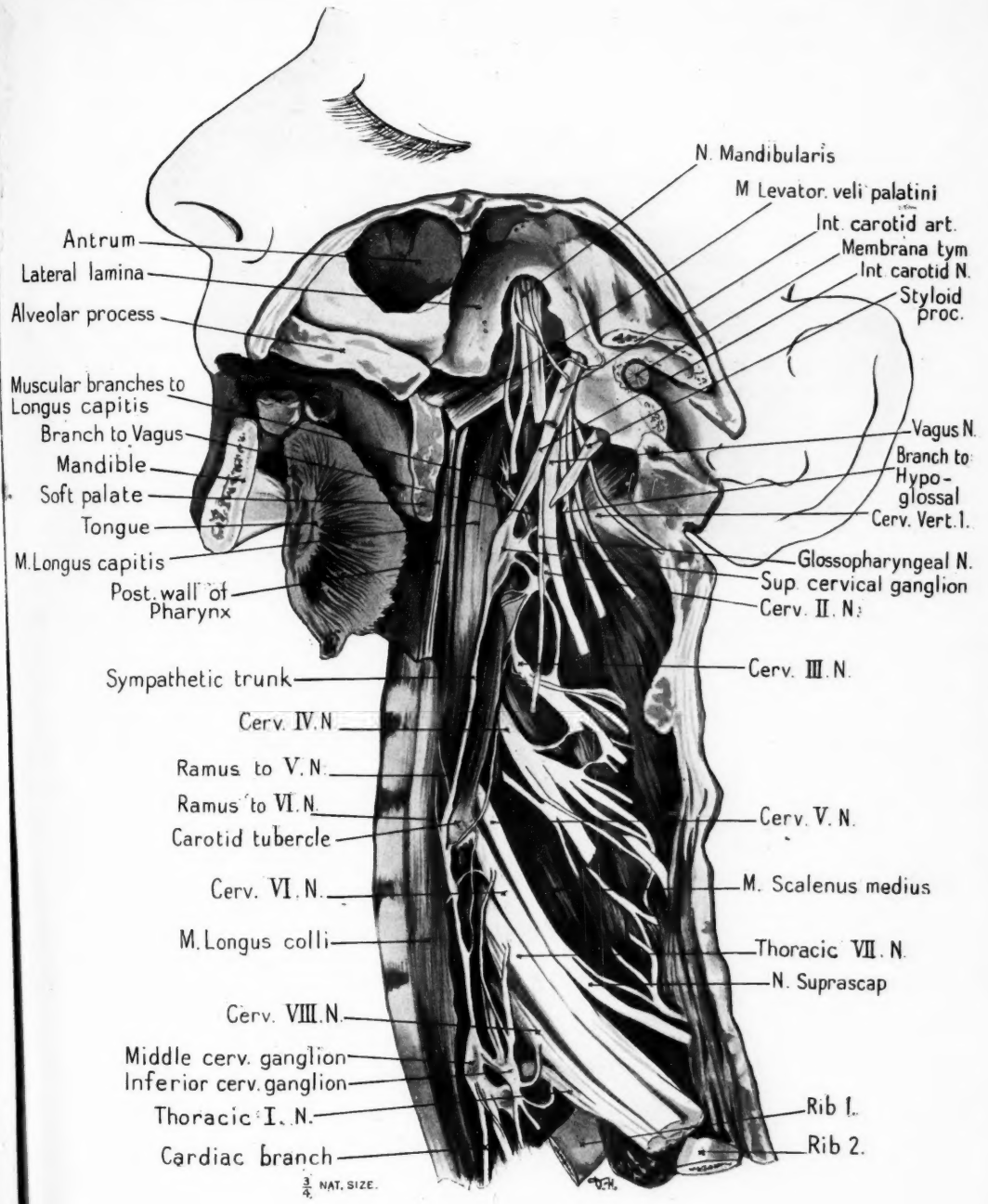
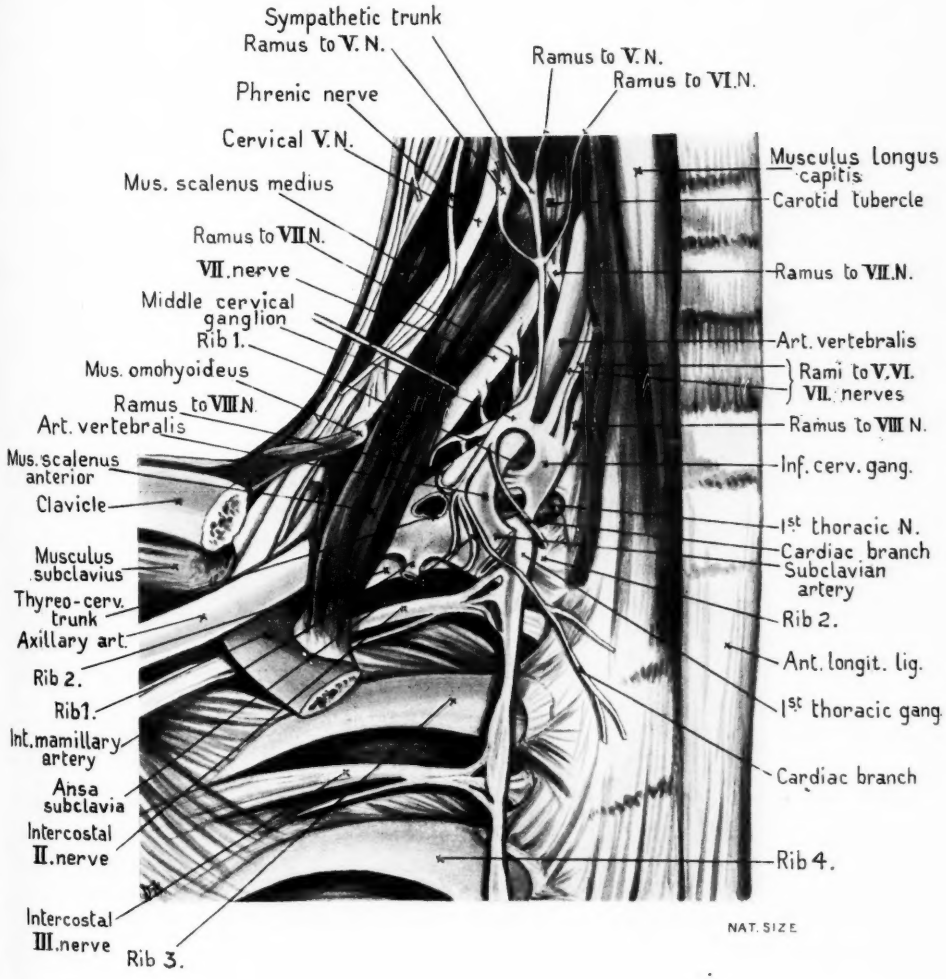
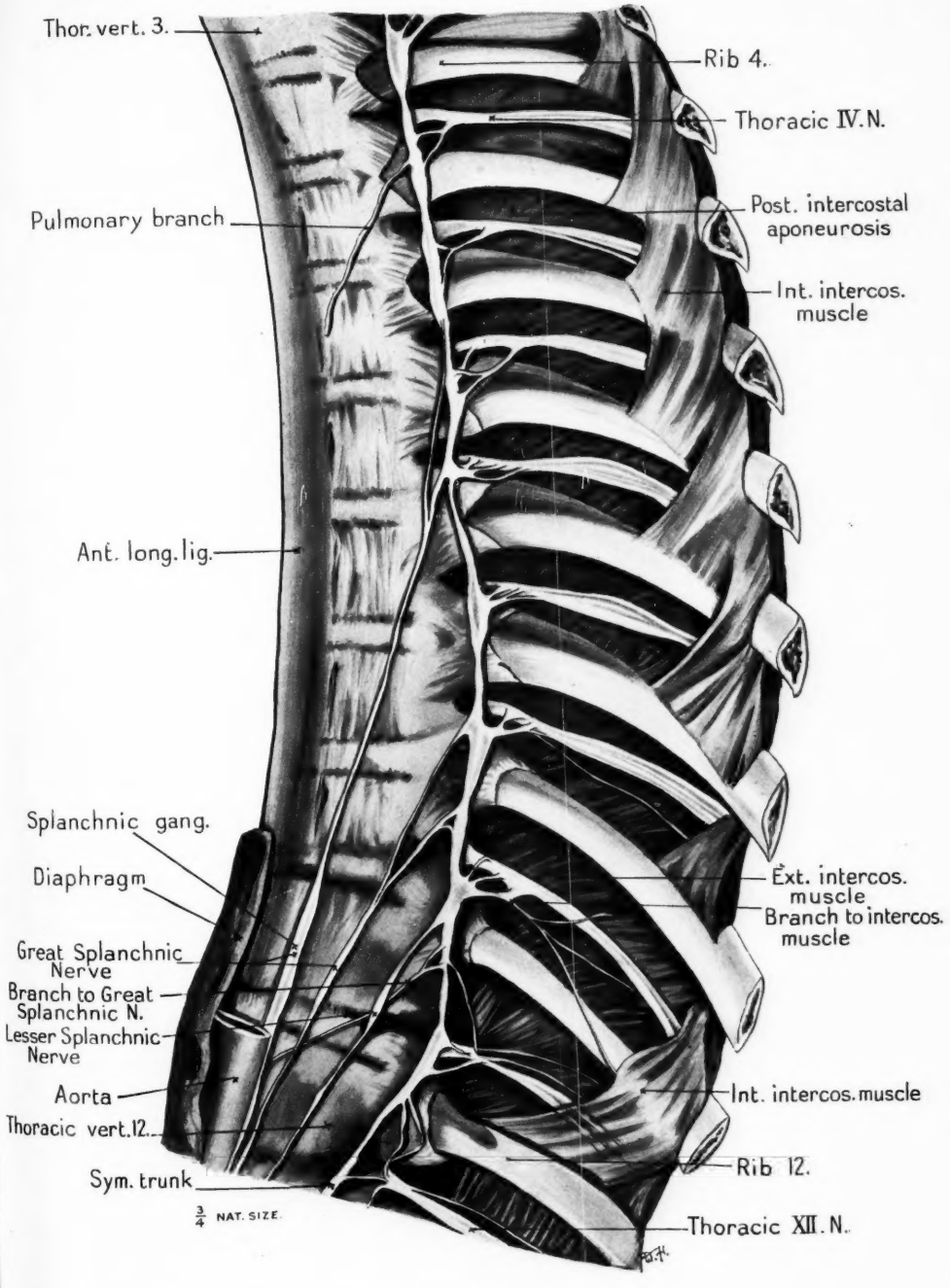
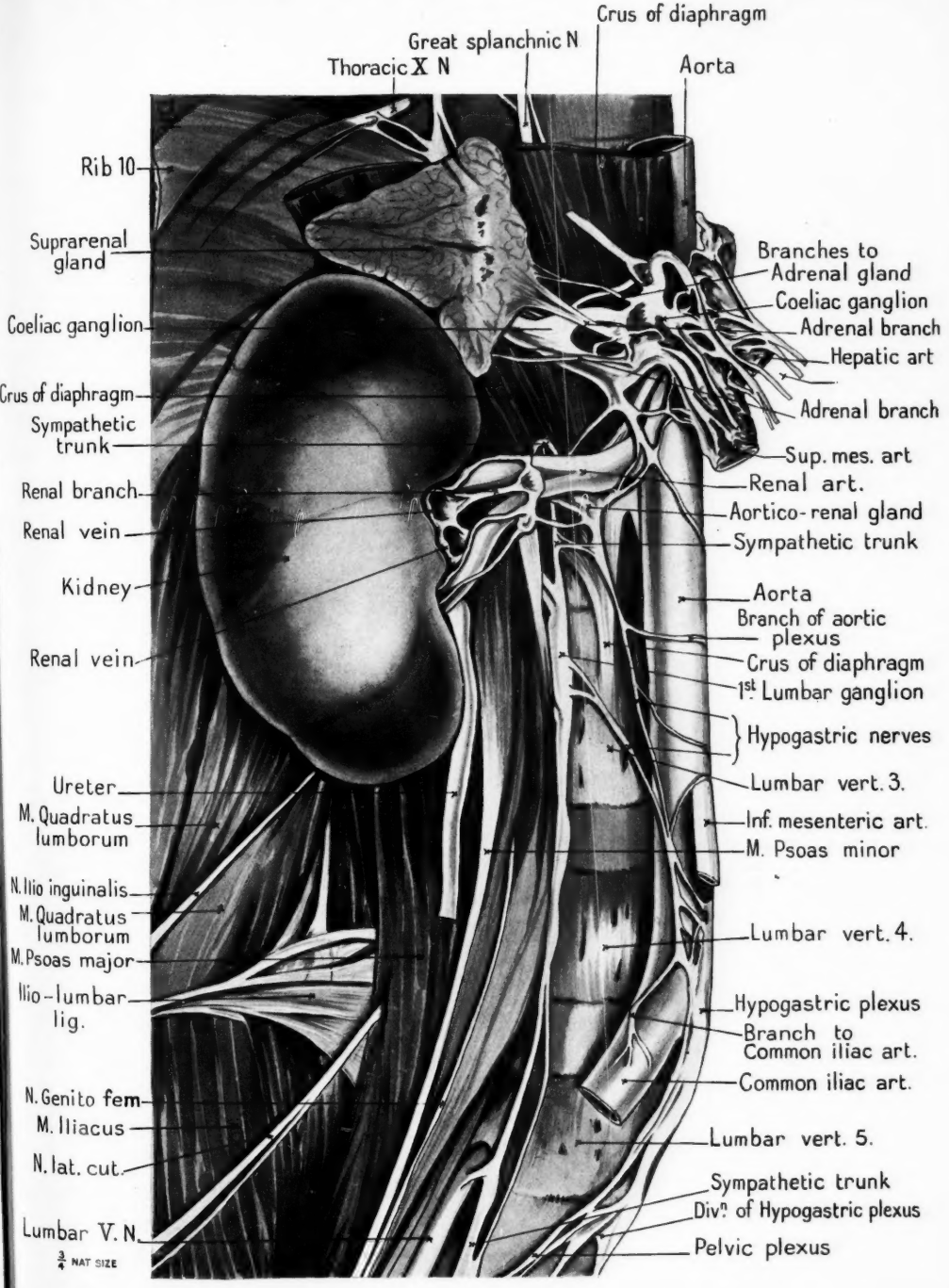
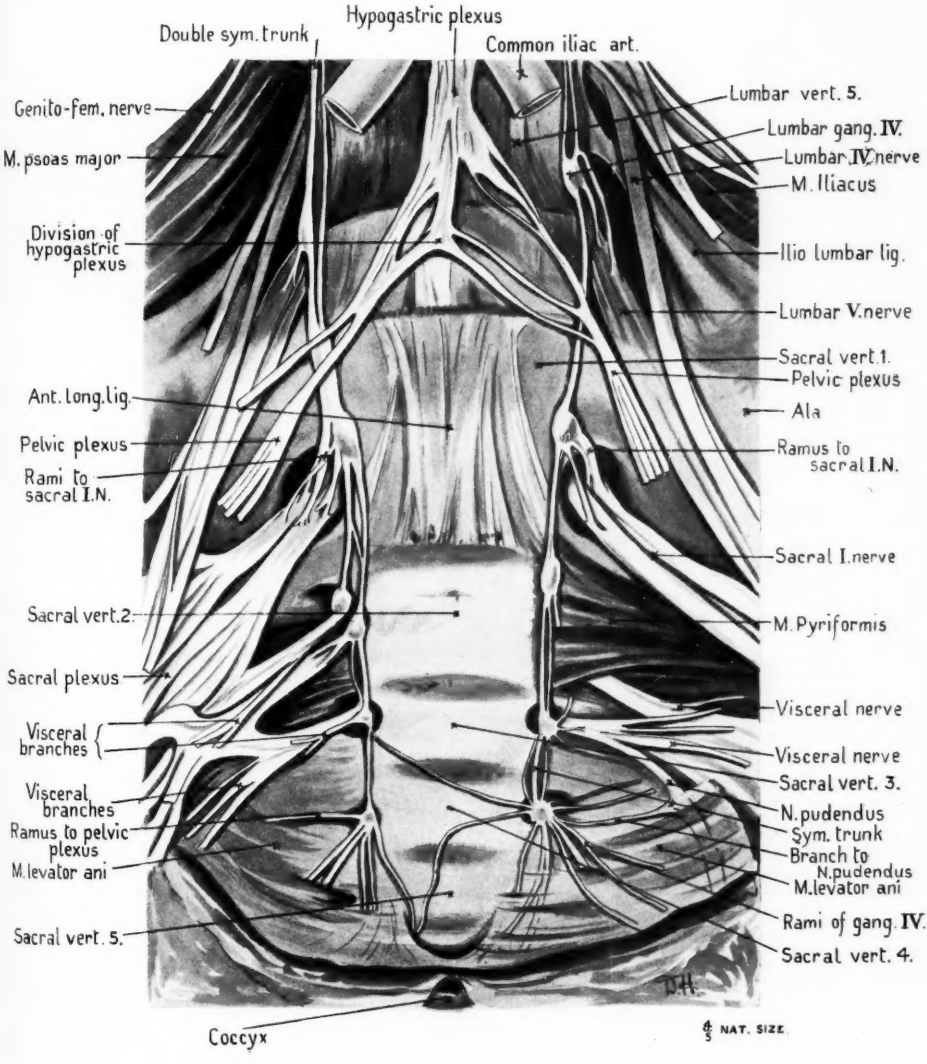

N. Mandibularis
M Levator. veli palatini
Int. carotid art.
Membrana tym
Int carotid N.
Styloid proc.
Antrum
Lateral lamina
Alveolar process
Muscular branches to Longus capitis
Branch to Vagus
Mandible
Soft palate
Tongue
M. Longus capitis
Post. wall of Pharynx
Vagus N.
Branch to Hypo-glossal
Cerv. Vert. 1.
Glossopharyngeal N.
Sup. cervical ganglion
Cerv. II. N.
Sympathetic trunk
Cerv. III. N.
Cerv. IV. N.
Ramus to V. N.
Ramus to VI. N.
Carotid tubercle
Cerv. V. N.
Cerv. VI. N.
M. Scalenus medius
M. Longus colli
Thoracic VII. N.
N. Suprascap
Cerv. VIII. N.
Middle cerv. ganglion
Inferior cerv. ganglion
Thoracic I. N.
Cardiac branch
Rib 1.
Rib 2.
¾ NAT. SIZE.

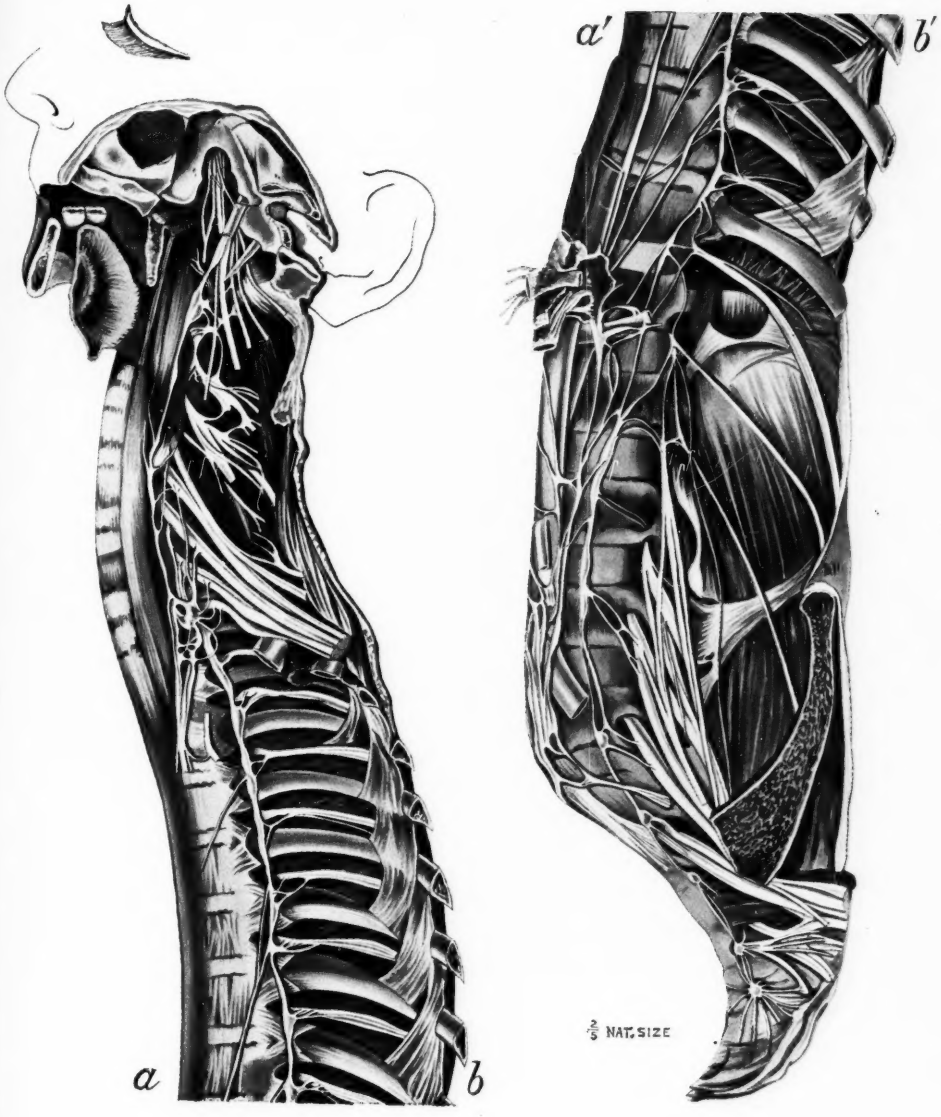

Sympathetic trunk
Ramus to V. N.
Ramus to V. N.
Ramus to VI. N.
Phrenic nerve
Cervical V. N.
Mus. scalenus medius
Ramus to VII. N.
VII. nerve
Middle cervical ganglion
Rib 1.
Mus. omohyoideus
Ramus to VIII. N.
Art. vertebralis
Mus. scalenus anterior
Clavicle
Musculus subclavius
Thyreo-cerv. trunk
Axillary art.
Rib 2.
Rib 1.
Int. mamillary artery
Ansa subclavia
Intercostal II. nerve
Intercostal III. nerve
Rib 3.
Musculus longus capitis
Carotid tubercle
Ramus to VII. N.
Art. vertebralis
Rami to V, VI. VII. nerves
Ramus to VIII. N.
Inf. cerv. gang.
1st thoracic N.
Cardiac branch
Subclavian artery
Rib 2.
Ant. longit. lig.
1st thoracic gang.
Cardiac branch
Rib 4.
NAT. SIZE

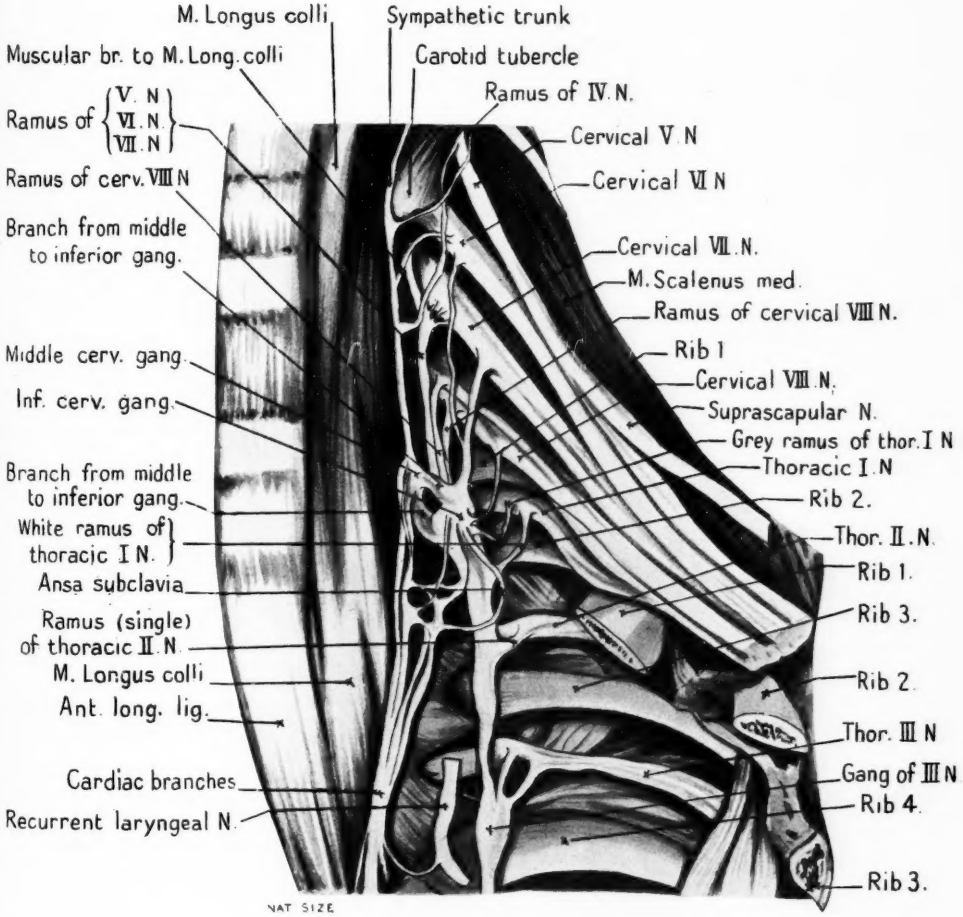

Thor. vert. 3.
Rib 4.
Thoracic IV. N.
Pulmonary branch
Post. intercostal aponeurosis
Int. intercos. muscle
Ant. long. lig.
Splanchnic gang.
Diaphragm
Ext. intercos. muscle
Branch to intercos. muscle
Great Splanchnic Nerve
Branch to Great Splanchnic N.
Lesser Splanchnic Nerve
Aorta
Int. intercos. muscle
Thoracic vert. 12.
Rib 12.
Sym. trunk
¾ NAT. SIZE.
Thoracic XII. N.

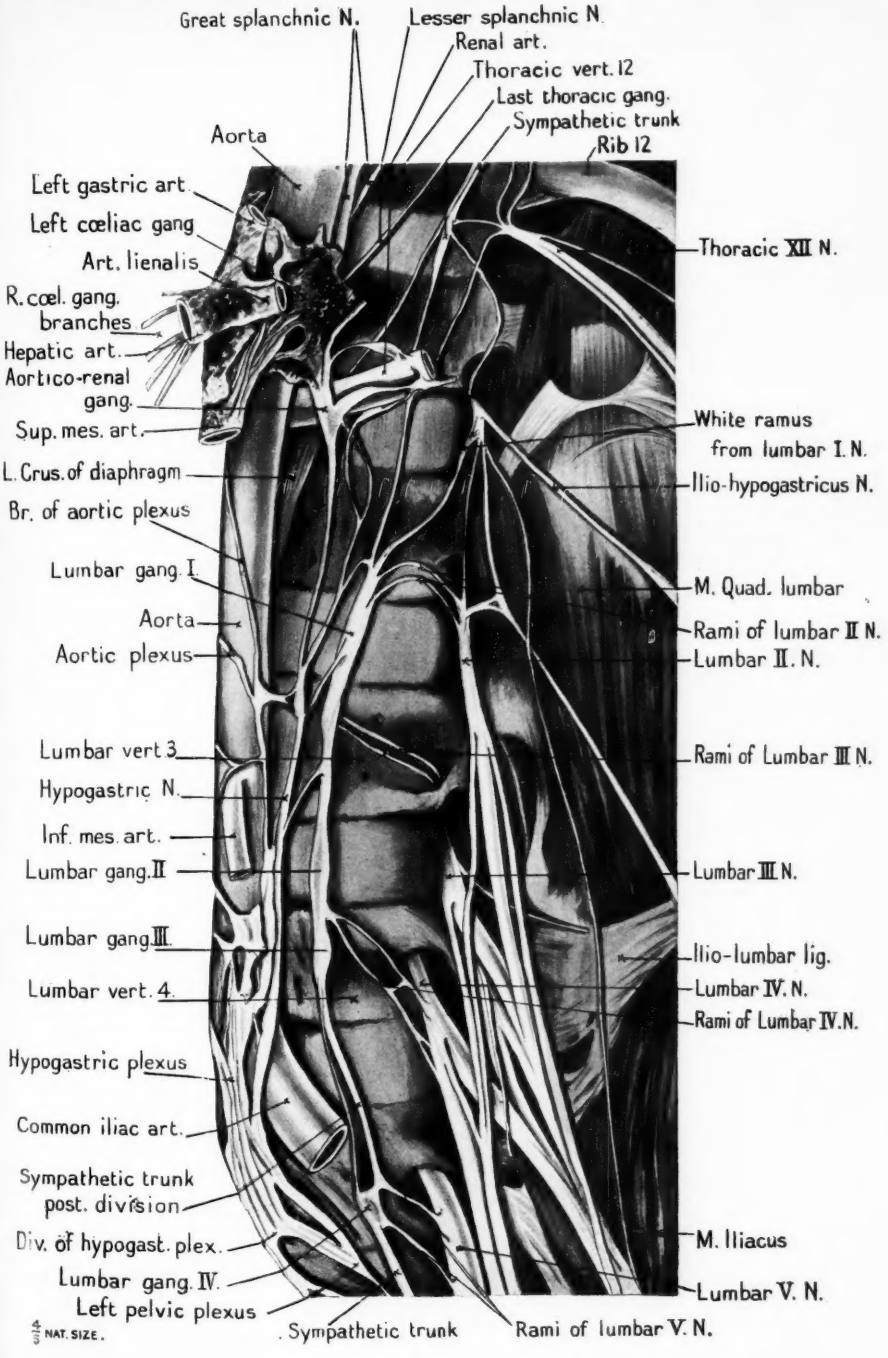


POTTS—HUMAN SYMPATHETIC NERVOUS SYSTEM


Double sym. trunk
Hypogastric plexus
Common iliac art.
Genito-fem. nerve
M. psoas major
Division of hypogastric plexus
Ant. long. lig.
Pelvic plexus
Rami to sacral I.N.
Sacral vert. 2.
Sacral plexus
Visceral branches
Visceral branches
Ramus to pelvic plexus
M. levator ani
Sacral vert. 5.
Coccyx
Lumbar vert. 5.
Lumbar gang. IV.
Lumbar IV. nerve
M. Iliacus
Ilio lumbar lig.
Lumbar V. nerve
Sacral vert. 1.
Pelvic plexus
Ala
Ramus to sacral I.N.
Sacral I. nerve
M. Pyriformis
Visceral nerve
Visceral nerve
Sacral vert. 3.
N. pudendus
Sym. trunk
Branch to N. pudendus
M. levator ani
Rami of gang. IV.
Sacral vert. 4.
D.H.
⅘ NAT. SIZE


a'
b'
a
b
⅖ NAT. SIZE


M. Longus colli
Sympathetic trunk
Muscular br. to M. Long. colli
Carotid tubercle
Ramus of IV. N.
Ramus of V. N VI. N VII. N
Cervical V N
Cervical VI N
Ramus of cerv. VIII N
Branch from middle to inferior gang.
Cervical VII. N.
M. Scalenus med.
Ramus of cervical VIII N.
Rib 1
Middle cerv. gang.
Cervical VIII. N.
Inf. cerv. gang.
Suprascapular N.
Grey ramus of thor. I N
Thoracic I. N
Branch from middle to inferior gang.
Rib 2.
White ramus of thoracic I N.
Thor. II. N.
Rib 1.
Ansa subclavia
Rib 3.
Ramus (single) of thoracic II. N
M. Longus colli
Rib 2
Ant. long. lig.
Thor. III N
Cardiac branches
Gang of III N
Recurrent laryngeal N.
Rib 4.
Rib 3.
NAT SIZE


Great splanchnic N.
Lesser splanchnic N.
Renal art.
Thoracic vert. 12
Last thoracic gang.
Sympathetic trunk
Rib 12
Aorta
Left gastric art.
Left cœliac gang.
Art. lienalis
R. cœl. gang. branches
Hepatic art.
Aortico-renal gang.
Sup. mes. art.
L. Crus of diaphragm
Br. of aortic plexus
Lumbar gang. I.
Aorta
Aortic plexus
Lumbar vert. 3
Hypogastric N.
Inf. mes. art.
Lumbar gang. II
Lumbar gang. III.
Lumbar vert. 4.
Hypogastric plexus
Common iliac art.
Sympathetic trunk post. division
Div. of hypogast. plex.
Lumbar gang. IV.
Left pelvic plexus
Thoracic XII N.
White ramus from lumbar I. N.
Ilio-hypogastricus N.
M. Quad. lumbar
Rami of lumbar II N.
Lumbar II. N.
Rami of Lumbar III N.
Lumbar III N.
Ilio-lumbar lig.
Lumbar IV. N.
Rami of Lumbar IV. N.
M. Iliacus
Lumbar V. N.
Rami of lumbar V. N.
Sympathetic trunk
⅔ NAT. SIZE.

DESCRIPTION OF PLATES

Plate I. Lateral view of the left cervical sympathetic trunk and its connections. The superior cervical ganglion has been displaced forwards slightly (⅔ nat. size).

Plate II. Front view of the lower cervical and upper thoracic region showing the sympathetic trunk and its connections (nat. size).

Plate III. Lateral view of the left thoracic sympathetic trunk below the level of the fourth rib (⅔ nat. size).

Plate IV. Lateral view of the right lumbar sympathetic trunk. The *vena cava inferior* has been removed (⅔ nat. size).

Plate V. Front view of the sacral portion of the sympathetic nervous system (½ nat. size).

Plate VI. Lateral view of the left sympathetic trunk and its connections (⅔ nat. size).

Plate VII. Antero-lateral view of the lower cervical and upper thoracic portions of the sympathetic nervous system on the left side to explain the structures shown in Plate VI in this region. The *musculus scalenus anterior* has been removed (nat. size).

Plate VIII. Lateral view of the left lumbar sympathetic trunk to explain the structures shown in Plate VI in this region. The *musculus psoas major* has been removed (½ nat. size).

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THE HISTOGENESIS OF BONE

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INTRODUCTION

Few processes in histogenesis have been the subject of so much controversy, as that of the development of bone. On reading over the literature, even incompletely, the conviction came with considerable force, that the chief cause of the inability of observers, to find agreement, lay in technical difficulties in obtaining satisfactory preparations for cytological study. The divergent opinions are accounted for by the singular absence of detailed work—a fact which has fostered and sustained a controversy into which there is no need to enter.

Microscopic evidence of cell growth and change is yielded by slight morphological variations in different individual cells. Slight differences in structure, and staining reaction, are the only factors by means of which variations can be determined. It is essential, with cells examined in a dead state, to have a standard of fixation which registers detailed and minute structure. Further, it is constantly to be borne in mind, that merely a phase of life is represented, through which the cell was passing at the time of its death. Especially is this so in actively growing, developing tissue, where many structural tendencies are manifested by the act of growth. Thus, in fixed primitive tissue, the ontogeny of any given cell is a matter of conjecture, and it can only be defined with any degree of certainty by an experienced observer.

It would be redundant to attempt an historical survey of the contributions to the problem of osteogenesis. Keith (18), beginning with Duhamel (7) and Haller (12), an hundred and fifty years ago, has traced the main advances in our knowledge of bone growth, from the experimental side. The former asserted the osteogenic function of periosteum, the latter, having observed the deeply placed epiphyseal centres, denied it. Keith writes: "After a century and a half of discussion we still have these two schools." The issue involved in this controversy is the origin of the osteoblast, essentially a cytological problem, dependent for its solution on the recognition of the osteoblast as a definite cell entity.

As far as has been possible, an attempt has been made to present descriptions of the processes studied in developmental sequence. Interpretation in terms of growth has been the object; rather than the mere recording of a series of microscopical phenomena of fixed tissue, a prevalent procedure, bereft of all meaning, inasmuch as living tissue comes to be regarded as though it were dead.

The results embodied in this research, in a measure find agreement with much that has been done hitherto, but of previous authors, Maximow's (24) is the more completely confirmed. The preparations, though obtained with a different technique, render similar cytological values, which in many respects yield a similar interpretation.

TECHNIQUE

Materials and methods. Rabbit, guinea-pig, cat, dog, and human foetal bones were examined. No essential differences, in the processes described, were found in these animals. Rabbits and guinea-pigs form more convenient material than other mammals, both because of the ease of breeding, and because of the small bulk of the tissue. The former are pre-eminently more suitable, foetal growth being extremely rapid, a gestation period of thirty days resulting in a full-time foetal animal, approximately the same size and weight as a full-time foetal guinea-pig, which has a gestation period of seventy days.

All types of cartilage bones were used in various stages of development, especially the short and long bones of the fore and hind limbs. Metacarpal and metatarsal bones are exceptionally satisfactory—small, and rapidly penetrated by fixatives: once the integument is removed, they require no further handling. Since the processes described are the same for all bones laid down in cartilage, no reference will be made to specially named bones.

For purposes of description and illustration rabbits and guinea-pigs are used.

The foetal animals were delivered through the abdominal wall, after killing the mother by fracture-dislocation of the neck. Tissue required was rapidly dissected and transferred to the fixative in as recent a state as possible.

FIXATION

Bulk tissue, consisting of bones freed from the surrounding skin and muscle, was fixed in a saturated solution of mercuric chloride in saline, at 37° C., to 100 c.c. of which ½ to 1½ c.c. of 1 per cent. osmic acid solution was added, immediately after introducing the tissue. To prevent vaporisation of the osmic acid, the specimen bottles were tightly corked. Long bones of more than 5 mm. in diameter were sectioned longitudinally. Ten to seventeen hours' immersion, depending on the size of the tissue, gives adequate fixation. If the quantity of osmic acid solution introduced is sufficient, the tissue becomes dark brown in colour. If left for a longer period, the mercuric chloride tends to make the tissue very brittle.

DECALCIFICATION

Foetal bones; rabbits, up to the termination of the gestation period, were transferred after fixation in Zenker's fluid (to which acetic acid was not added) or Müller's fluid, for 12 to 24 hours. This treatment serves a double purpose, both decalcifying young bone, and acting as a satisfactory mordant, especially if azur stains are subsequently used.

Perenyi's solution was found to be the most suitable reagent for the decalcification of more mature bone. If not used too long, the cell preservation is not affected; a small amount of shrinking obscures the finer detail, but does not interfere with the identification of the different cell elements.

TEASED AND SMEAR PREPARATIONS

These were treated with the above fixative for 10 minutes, and then transferred to Zenker's fluid for a further 10 minutes. Osmic acid vapour was also used for smear preparations, in which case Mallory's triple connective tissue stain was found to give very satisfactory results.

EMBEDDING

Paraffin and celloidin were both employed. For paraffin embedding, the tissue was passed through graduated spirits, beginning at 30 per cent., and rapidly ascending through 50, 60, and 70 to 80 per cent., hardening in the latter for 8 to 12 hours, finally ascending to absolute through 90 per cent. alcohol, using two changes of the former over a period of 4 hours.

Cedar wood oil was used in two changes over 72 hours, for removing the alcohol.

The tissue was then transferred direct to paraffin with a melting point either of 49° or 52° C. Indifferent results may be anticipated if the paraffin is permitted to pass above 56°. Four baths of paraffin over 12 hours remove the cedar wood oil.

The thin sections obtained with the paraffin afford a considerable advantage over the celloidin method.

STAINING

Eosin and azur, or Wright's (23) polychrome methylene blue, and eosin, give good results. The least capricious staining was obtained with 5 per cent. aqueous eosin and Grübler's polychrome methylene blue $\frac{1}{4}$ per cent. differentiated in 3 per cent. colophonium in 95 per cent. alcohol (after Wright). This stain is especially good for cytological work when employed after the fixation described above.

THE FORMATION OF THE CARTILAGE MODEL

The primitive connective tissue of the chondrogenetic areas originally forms a syncytium resembling Wharton's jelly. The cellular elements increase and eventually form a dense packed mass. Geddes (10) and Mall (22) have separately described the process of this condensation. At this stage it is not possible to differentiate between the cells which ultimately form the muscle and perimysium, and those which form the cartilage model and perichondrium. The varying growth potentials inherent in the cells express the resultant tissues by group change. In the chondrogenetic area, there appears a condensation, followed, first by an enlargement, then by a separation of the cells, resulting from the deposition of chondromucin as an exoplasm (Fig. 1).

Growth of the cartilage area, thus formed, ensues by peripheral increments, the adjacent close-packed mesenchymal cells undergoing transformation by secreting chondromucin, and thereby collectively contributing to the development of the cartilage model. Apart from enlargement, this cytomorphosis is not marked by any special change in the primitive connective tissue cells. The appearance of the chondromucin is the essential feature of the transition. In its own increase, the mesenchyme is exceedingly active. Cell division in the new-formed cartilage is also a frequent appearance. Free movement following division is apparently not impeded to a greater extent than in less dense tissue. Later, it will be seen that the capacity of the cartilage cell, to move freely in its matrix, is the causal factor in effecting the growth of diaphyseal bone longitudinally.

Finally, a cartilage mass arises, assuming, in broad outline, the shape of the bone which eventually replaces it.

Concurrently with the growth of the cartilage, muscle and perimysium appear, arising from the same type of connective tissue energid.

As the cartilage model nears completion, part of the surrounding mesenchyme immediately subjacent to the perimysium and muscle undergoes a transition into loose cellular fibrous tissue. In this way the zone of the primitive connective tissue becomes delimited forming cartilage centrally and fibrous tissue peripherally. Both the mesenchyme and the fibrous tissue which arises from it are usually grouped together under the one term—perichondrium. The confusion arising from this use of the term, will be considered later. Joint cavities arise by cleavage of the mesenchyme (Fig. 2), and by isolation following cleavage, the joint menisci are formed. Capsular tissue appears in continuity with the loose fibrous tissue previously described.

THE PERICHONDRIUM

In the previous paragraph, the current use of the term perichondrium was questioned. It was shown that the chondrogenetic mesenchyme undergoes two divergent growth transitions, viz., the formation of cartilage and the formation of fibrous tissue, the undifferentiated mesenchyme persisting between these specialised structures. Its cells are characterised by a large ovoid vesicular nucleus, with chromatin granules embedded in the nodes of a network of fine chromatin threads. The granules vary in size, the larger resembling nucleoli. Cell boundaries are not apparent, the tissues having the appearance of a syncytium. Whether it is or not, is rendered indeterminate by the close packing of the cells which tend to lie with the long axis of the nucleus parallel to the long axis of the cartilage model. At this stage it forms a very definite zone, readily identified by its pale appearance, contrasted with the intense basophilia of the tissues on either side. Progressively, capillaries appear in it, recognised by their lumina, containing red blood corpuscles, the endothelial cells so resembling the cells of the mesenchyme that it is impossible to consider them separately.

The peripheral fibrous tissue is quite otherwise, though it merges with it, all transition forms, from the young connective tissue cells to elongated flattened fibroblasts embedded in connective tissue fibrils, being readily observed (Fig. 3). It is to this tissue that the term perichondrium is here applied, denoting a structure which arises by an end differentiation of the subjacent indifferent primitive connective tissue cells. It will hereafter be demonstrated that by a change in name, concurrently with changes in the subjacent mesenchyme, the perichondrium becomes the periosteum.

THE PERIOSTEUM

Duhamel (7) originally attributed an osteogenic function to the periosteum, ascribing circumferential increase in the long bones to it. Later, Goodsir (11), from a pathological standpoint, on considering the case of new bone, enveloping a necrosed shaft, resulting from osteomyelitis, came to the conclusion "that periosteum does not possess an independent power of forming osseous tissue." Contributing extensively to this view, is the evidence of MacEwan (20) in his treatise *The Growth of Bone*, an experimental enquiry into the development and reproduction of diaphyseal bone, together with the experience of three or four decades of experimental surgery. He has demonstrated conclusively, that bone may live without its periosteum, and further, that bone as a separate tissue is capable of extensive proliferation.

Interstitial growth, MacEwan regards as a potentiality of bone tissue, for example, when a peg is driven into bone and subsequently removed, the resultant gap is filled by the proliferation of the surrounding osseous tissue. Circumferential thickening, he describes as a manifestation of interstitial growth.

Much evidence has been produced in favour of Goodsir's and MacEwan's contention that periosteum is merely a "limiting membrane." Gallie and Robertson (9) have confirmed MacEwan's work.

Morley (25) has produced experimental traumatic myositis ossificans by denuding areas of bone by removing periosteum, then crushing the neighbouring muscles. He affected a cure by grafting autogenous fascia over the denuded areas.

MacEwan has also observed that in fractures, when the periosteum is torn, more callus is thrown out than in cases where the membrane is intact.

Keith and Hall (19), in a study of the infection and repair of bones in the War Office collection, resulting from the European War, 1914–1918, have found bone masses devoid of periosteum forming new bone.

From this evidence it may be assumed, that periosteum is not essential to the regeneration of bone, but on the other hand, it definitely acts as a limiting membrane.

Histological evidence discloses osteoblasts in the subperiosteal region, from which it might be inferred that they come either from the periosteal tissue or from the bone. MacEwan (20) and Gallie and Robertson (9) contend that these osteoblasts come from the Haversian canals.

Any problem of tissue formation is essentially a cytological problem. Experimental evidence leads mainly to an appreciation of function. Appreciation of structure is dependent on a study of the cytomorphosis of the cell elements from which a tissue is derived.

It has been shown that the primitive connective tissue cells, of the chondrogenetic areas, evolve into two definite tissues, cartilage centrally, and fibrous perichondrium peripherally, the mesenchyme persisting between these two tissues. At the stage of the fully developed cartilage model, the fibrous zone is well marked, although the transition between it and the mesenchyme is still evident. Hereafter, the mesenchyme is better studied in tangential sections as the cells are only a few layers deep.

At the site of the cartilage changes, preparatory to endochondral ossification, the mesenchyme becomes sharply delimited, no longer contributing to the growth of the cartilage model. This cessation in the formation of chondroblasts is soon followed by the formation of osteoblasts.

The perichondrium is continually growing during this period mainly by division and increase of its own fibroblasts rather than by contribution from the mesenchyme.

Bone deposition first appears as a peripheral splint round the cartilage model at the site of the enlarging cartilage cells. Thus, four zones can be recognised at this stage, viz., bone substance, a layer of osteoblasts, primitive connective tissue cells of the persisting mesenchyme, and finally, the cellular fibrous tissue of the perichondrium or periosteum, the change in name coinciding with the appearance of bone substance. Thus, the mesenchyme at this stage still shows two growth activities—the formation of osteoblasts and continued increments to the periosteum.

Regarded from the point of view of its development, the periosteum is an end differentiation of primitive connective tissue forming a limiting membrane for the tissue from which it is derived and blending intimately with it. Close-packed, elongated, flattened fibroblasts with well developed connective tissue fibrils constitute its structure at this period (Fig. 4). Superiosteal ossification proceeds with the continued formation of osteoblasts from the primitive connective tissue cells. At later stages, towards the completion of bone growth, the periosteum appears as a fully developed fibrous membrane, beneath which occasional osteoblasts and undifferentiated connective tissue cells are found. It is thus apparent that two totally different histological pictures of the periosteum are presented at the two extremes of its growth.

Early in its development, when more cellular than fibrous, it shows a direct continuity with the osteogenic mesenchyme, an appearance which has led to the prevalent conception of the osteogenic function of periosteum.

Considered through the various stages of its growth, in its relation to the chondrogenetic and osteogenic mesenchyme, it is clearly a structure which appears as the end development of primitive connective tissue, and is in no way directly associated with bone formation.

THE OSTEOBLAST

The varying points of view, put forward concerning osteogenesis, have arisen from a consideration of the possibilities of the origin of the osteoblast, rather than from an intimate study of the morphogenesis of the cell itself.

Almost any histological technique discloses, in embryonic bone, a pavement of cells with no characteristic value, arranged subperiosteally, and along newly-formed bone trabeculae; obviously associated with the presence of the bone. Prolific though the literature is on this subject, Maximow (24) alone has ventured to ascribe definite characteristics, distinguishing the osteoblast from other connective tissue cells. Inasmuch as the cell under discussion has lacked identity, apart from its relation to recently formed bone, so have many other cells in embryonic osseous tissue been a mystery, concerning which, suggestion rather than evidence has been the feature of the conclusions of many.

Geddes (10) suggests a possible ectodermal origin for the osteoblast. Retterer (26), MacEwan (20), and many others have produced evidence in favour of the cytomorphosis of the cartilage cell following the hypertrophic stage. Apart from his work on the antlers of deer, MacEwan's (21) evidence is negative for the periosteum rather than positive for the cartilage cell.

Others conclude simply that the osteoblasts arise from the periosteum or perichondrium: Jackson (16), Hamar (13), etc.

Todd (28), on the other hand, states that the osteoblast is a transformed fibroblast, which may, or may not, have passed through the chondroblast stage.

The first appearance of the osteoblast has been shown to occur around the zone of the cartilage activity, which precedes the invasion of the mesenchyme into the diaphysis of the cartilage model. Concurrently with the changes in the cartilage cells they evolve from the subperichondral mesenchyme and begin bone deposition (Fig. 5), forming an osseous splint for the rapidly weakening cartilage structure (Fig. 6). At this initial site of bone deposition, the change in the mesenchyme is characterised by increased vascularity and increased multiplication of the young connective tissue cells.

Whether the capillary endothelium is derived from pre-existing endothelial cells which have penetrated from without, or from the mesenchymal cells *in situ*, is not easy to determine, from fixed preparations. The nuclear structure in both types of cell is identically the same. Reference will again be made to the origin of the endothelium, when considering the invading osteogenic mesenchyme of the intra-trabecular areas in the cartilage.

The evolution of the osteoblasts from the young connective tissue cells is represented by a series of characteristic transition phases. Tangential sections illustrate the process very clearly, by extending the area of transition (Fig. 5). A loosening of the cells of the apparent syncytium occurs, those nearest the cartilage becoming completely discrete. Increase in the size of the nucleus and bulk of the cytoplasm, together with a more basophil reaction in staining,

is associated with the separation phase. The cell body then elongates, the nucleus moving eccentrically to one or other pole. One or two aggregations appear in the nucleus, resembling nucleoli.

Associated with the eccentric movement of the nucleus, a spherical pale area, relatively the same size as the nucleus, makes its appearance in the centre of the cytoplasm. Maximow (24) has observed this structure and termed it the "Sphere." From the analogy of the attraction sphere seen in the haemoblast with the same technique, it appears justifiable to assume that the area referred to in the osteoblast is a similar structure. It is best seen when the osteoblast is sectioned in its long axis (Fig. 7). Frequently the cell is so cut in sectioning that the "sphere" appears in the midst of the cytoplasm unrelated to the nucleus, resembling a degenerated nuclear mass.

The fully formed osteoblasts are remarkable for the density of their basophilia, both in the cytoplasm and nucleus. It is a progressive phenomena increasing throughout the development of the cell.

CHANGES IN THE CARTILAGE MODEL PRIOR TO OSSIFICATION

The successive phases in the activity of the cartilage cell, preceding endochondral ossification in the diaphysis, are well known, but since the fate of the cartilage cell has not been a subject in which unanimity has been attained, a restatement in respect of this issue is warranted. Further, a long bone depends on cartilage growth for its increase in length—a rôle usually ascribed to the cartilage but incompletely stated.

The first cells to manifest any group activity in the cartilage model are situated in the centre of the diaphysis. They merely undergo a process of hypertrophy whereby the chondromucin matrix is modelled into a meshwork of attenuated trabeculae enclosing the enlarged cartilage cells (Fig. 6). Invasion by the peripheral mesenchyme then takes place, the trabeculae in the line of advance undergoing solution, by the young connective tissue cells. The zone of hypertrophy extends in two directions towards both epiphyses (Fig. 8). At the same time, the process becomes slower, exhibiting a characteristic ordered arrangement which persists in the "diaphyseal plate" (Appendix II) until the termination of the growing period. Different phases of enlargement are represented by zones to which Retterer (26) has applied the descriptive terms used in this work.

The resting cartilage cells undergo multiplication by mitosis, each new cell separating and becoming completely reinvested with chondromucin. Separation apparently takes place in two planes, daughter cells moving in the transverse plane so that groups of three to six appear in transverse section. The main movement, however, is in the long axis of the bone, where the cell groups are seen arranged in rows (Fig. 9). The flattened appearance of the individual cells of each group in this serial zone is remarkable. The cells are considerably larger than the inactive cells, lying with their long axis transversely to the diaphysis (Fig. 9). Though closely aligned with one another,

filamentous strands of chondromucin separate each cell. By the arrangement in rows, longitudinal cylinders of chondromucin are formed, isolating each cell group.

Progressive enlargement ensues, each cell ultimately attaining a size where all its diameters are commensurate with the transverse diameter of the flattened phase.

In this way the cell groups effect a continuous growth, registered by the extension of the longitudinal trabeculae between the cell groups. The measure of growth thus depends on the rate of division in forming the groups, and further, on the velocity of enlargement of the cells, collectively. Increments to the length of a developing bone are thus contributed by this activity of the cartilage cell. During enlargement, maturity is attained and degeneration supervenes. In rapidly growing animals, e.g., the rabbit, they attain a size of 40 to 80μ, collectively forming the hypertrophic zone of Retterer. Degenerative processes are the features of the hypertrophic cells. They stain faintly with orthochromatic reaction, during the phase of enlargement. The nucleus becomes swollen: in bulk preparation it resembles a bubble, the chromatin becomes sparse and eventually disappears; finally, the only evidence of a nucleus being a thin distended nuclear membrane. Vacuoles appear in the cytoplasm followed by an oedematous phase. In sections, the cell is ultimately represented by a shrunken granular mass of protoplasmic débris.

In the earlier stages of this investigation, evidence of the persistence of the cartilage cell was sought. The hypertrophic cells were isolated, rapidly fixed in Carnoy's solution, and stained with Weigert's haemotoxylin and Van Gieson's stain. No evidence of cytomorphosis was obtained. They persistently showed the appearance of old mature cells with all signs of structural degeneration.

The cell groups developed in the serial zone, persist in the hypertrophic zone, maintaining their relative positions, the rows still being separated by the longitudinal trabeculae which at this stage become calcified (Fig. 8).

The trabeculae separating the cells of a group become exceedingly attenuated during the process of cell enlargement, and undergo solution when the mesenchyme penetrates, offering little resistance to the actively growing young tissue.

The stouter longitudinal trabeculae persist, having registered the growth activity of the cartilage cell, forming a scaffolding on which the osteoblasts build.

Osteoblastic activity is a secondary process independent of the cartilage as such, merely consolidating the calcified chondromucin trabeculae, after the growth increments have been completed. Serial grouping and hypertrophic enlargement occur throughout the growing period of every diaphysis, the diaphyseal plate representing the remains of the cartilage model, ceaselessly preparing increments of calcified chondromucin to receive the deposition of ossein.

CHANGES IN THE CARTILAGE CELL OF THE EPIPHYSIS

After diaphyseal ossification has begun, the epiphysis continues to grow as a cartilage mass, for a period definite for every bone of each species. Increments arise in two ways; by cellular proliferation, and by new formation of cartilage, derived by transition from the subperichondral mesenchyme. The latter process ceases after the formation of the joint capsules and ligaments. All subsequent growth results from cartilaginous proliferation, both in the diameter of the diaphyseal plate, and the peripheral cartilage of the epiphyseal mass. It is thus seen that the growth impulse affecting the shape, size and form of a bone is inherent in the cartilage cells, both in the diaphysis and the epiphysis. Bone formation is a secondary process of replacement and consolidation, following in the wake of the cartilaginous growth.

The earliest change manifested in the cartilage of the epiphysis, is a mesenchymal penetration from the subperichondral zone. This occurs at several points immediately beyond the diaphyseal plate. Small areas of increase in the primitive connective tissue cells of the mesenchyme are followed by a local solution of the chondromucin apparently affected by the action of the chondroblasts. Channels are thus formed, beginning at the periphery, and extending into the centre of the cartilage. The young connective tissue cells of the subperichondral mesenchyme pass along these channels, carrying with them capillaries. The freed cartilage cells merge with the invading tissue and are eventually indistinguishable (Figs. 10, 11, 12). In the centre of the cartilage mass anastomoses take place, between the converging channels, forming relatively large spaces, filled with vascular primitive connective tissue.

In this manner the osteogenic mesenchyme gains the centre of the epiphysis, and awaits the opportunity for further development which is initiated by similar preparatory changes, already described for the cartilage cells in the mesenchyme. As in the diaphysis, group formation is not at first obvious, the hypertrophic stage being reached by scattered masses of cells related to the mesenchymal spaces (Fig. 9). Later, when the cell groups appear, they arrange themselves radially around the original ossific areas. The subsequent process is a continual replacement, of the spaces occupied by the dead hypertrophic cells, by the proliferating osteogenic mesenchyme, the ossification line forming the circumference of a circle with a continually increasing radius.

THE INVASION OF THE DIAPHYSIS OF THE CARTILAGE MODEL BY THE OSTEOGENIC MESENCHYME

Primary paths of ingress result from gaps that occur in the osseous splint deposited by the first formed subperichondral osteoblasts. Inroads into the cartilage are further made by the actively growing young connective tissue, dissolving the thin trabeculae of the chondromucin capsules, then invading and occupying the spaces occupied by the hypertrophic cells. At this stage there is no regularity in the process (Fig. 6). Islands of hypertrophic cells become

isolated, and certain of them are liberated from their spaces before degeneration (Fig. 13). Eventually, the original hypertrophic zone becomes replaced by the new tissue.

With the subsequent ordered enlargement of the cartilage cells, the new tissue conforms to a more regular advance, forming a growing zone of primitive connective tissue moving into the area occupied by the grouped hypertrophic cells, leaving in its wake the cell elements which develop from it. In later stages, the primitive connective tissue is only to be found, in its indifferent and undifferentiated state, closely applied to the ossification line, advancing continually by proliferation into the space occupied by the depleted cartilage cells.

THE OSTEOGENIC MESENCHYME IN ENDOCHONDRAL OSSIFICATION

The term "osteogenic mesenchyme" is here used to denote the primitive connective tissue, previously referred to under that name. Not only, however, are the elements concerned in endochondral ossification derived from it, but also the cells which initiate haematogenesis. The cytomorphosis resulting in blood formation will be considered in a subsequent work, but inasmuch as the primitive blood cell, "the haemoblast," makes its appearance shortly after the formation of the osteoblast, reference to it will be made to complete the histological picture.

The evolution of the osteoblast proceeds on precisely similar lines, in endochondral ossification, as previously described for subperiosteal ossification. The process, however, is more apparent owing to the less dense packing of the cells. At the point of advance the young connective tissue cells form a syncytial mass, eroding the fine trabeculae of the hypertrophic capsules and enveloping the débris of the dead cartilage cell (Fig. 14). Having filled the capsular spaces, the more peripherally situated cells become discrete and evolve into fully formed osteoblasts, these appearing, with the eccentric nucleus, large nucleus, and characteristic "sphere," aligned along the persisting calcified chondromucin trabeculae (Fig. 18). In the polychrome methylene blue and eosin preparations, calcified chondromucin stains a deep blue, and ossein a bright pink. This contrast serves in the detection of the first traces of deposited bone, which is seen as soon as the osteoblasts are observed arranged along the trabeculae (Fig. 15).

The capillaries also make their appearance among the young connective tissue, at the growing point. Endothelial cells arise directly from the mesenchymal cell, separating to form lumina into which red blood corpuscles flow (Fig. 16). The formed vessels occupy a central position in the inter-trabecular areas, around which the young connective tissue cells aggregate, forming a reticulum. From these cells the haemoblast arises and straightway proceeds with the genesis of the blood cells (Fig. 17).

Osteoclasts or polykaryocytes appear at an early stage along with the osteoblasts. The manner in which they arise will be dealt with later.

The above description applies to the changes that arise in the mesenchyme at the ossification line. In the initial invasion, however, the young connective tissue cells form a reticulum in which only osteoclasts are found, the evolution of the haemoblast occurring at a later stage. Hamar (13) refers to it as the primary marrow.

It is interesting to note that Dantschakoff (3), in her work on avian osteogenesis, figures the extensive commingling of cartilage cells and young connective tissue cells. Only in the canalisation of the epiphysis has it been possible to trace this, and then the cartilage cell in question is a young chondroblast, which has not undergone the characteristic changes preparatory to ossification.

THE OSTEOCLAST

Howell (14) originally distinguished two types of giant cells in bone, the megakaryocyte and polykaryocyte. Lately, Jordan (17) extended this classification into three types:

Megakaryocytes.
Polymorpho-nuclearkaryocytes.
Polykaryocytes.

He regards the megakaryocyte as a giant haemoblast, and the polymorpho-nuclearkaryocyte as a derivative, but since the latter is only a stage in the ontogenetic development of the former, and is the original megakaryocyte of Howell, confusion can only arise by the introduction of a new term.

The megakaryocyte has a haemogenic origin, and, by virtue of its size and polymorph nucleus, its appearance is always characteristic (Fig. 19). Protean in form, either basket shaped, crescentic, or annular, the nucleus is always vesicular with abundant chromatin network. Grouped, or scattered in the central area of protoplasm, a number of centrioles appear. Several diverse functions have been ascribed to it; erythropoiesis by Jordan (17), phagocytosis by Dickson (5); Wright (30), supported by Woodcock (29) and others, regards it as a source of the blood platelets.

The polykaryocyte is a multinucleated mass, concerning the origin of which many suggestions have been made.

Jordan (17) describes two types, with no genetic relationship. The first (derived from his megakaryocyte), haemogenic in function, forming endogenous red blood corpuscles, as plastids; the second type corresponding to the osteolytic osteoclast, to be described.

Jackson (16) and Maximow (24) describe a reticular origin for the osteoclast, regarding it as a phagocyte.

Arey (1) regards them as fusion products of depleted osteoblasts. He also concludes they are phagocytic.

Jordan's haemogenic type has not been observed, hence Howell's classification is accepted in this work.

The polykaryocyte or osteoclast is found wherever bone is present, but the megakaryocyte is peculiar to mammalian bone marrow. There is a striking

resemblance between the osteoclast and other multinucleated cells of the foreign body type, and the same issues are raised by different authors as to their origin. Some attribute their development from repeated mitosis or amitosis of the nucleus of individual cells, without division of the cytoplasm; Jackson (16), Dantschakoff (3) and Maximow (24) contend, that they arise by the confluence of mononucleated cells, without division of nuclei. The material investigated confirmed the latter view.

They originate early, at the stage when the connective tissue grows into the cartilage. The reticular cells from which they arise are of the young connective tissue type; these become grouped together and fusion cements the proximity (Fig. 20). They develop similarly in the zone of advancing connective tissue cells forming masses of protoplasm containing several nuclei, ranging from three to ten when seen in section (Fig. 21). Teased preparations from the rabbit show as many as 40 nuclei.

The shapes and forms are varied. Sometimes they are rounded or oval (Fig. 22), but more frequently angular (Fig. 23), or elongated with protoplasmic communications passing to neighbouring cells; osteoblasts, or reticular cells. Most frequently they are seen in apposition with the newly-formed bone trabeculae, which, in the process of growth, are absorbed, thereby extending the medullary cavity. They often occur lying freely in the inter-trabecular areas, or as syncytial masses bridging the gaps which have been made in the trabeculae. Occasionally, they are seen in the subperiosteal areas, apparently arising *in situ* from the local mesenchyme. During the process of formation, alterations occur in the nuclei and protoplasm of the cells from which they are developed. The slight basophilia of the protoplasm of the young connective tissue cells increases; the nuclei enlarge, the chromatin network becomes granular and a large nucleolus arises (Fig. 24). Young osteoclasts are generated in a zone where both deposition and absorption are features of bone growth. From their almost constant relation to trabeculae undergoing absorption, it is impossible not to ascribe to them an osteolytic function, though, on the other hand, it is difficult to conceive that the osteoblast is not fully capable of controlling the solution of its own exoplasm. The manner in which the osteoclast accelerates bone absorption has yet to be determined.

Mature forms are found in the haemogenic areas, with reticular protoplasm and diminished basophilia. Some of them develop vacuoles, the nuclei enlarge and become orthochromatic, finally, their fate is sealed by complete disintegration. Others seen in the same areas appear to split up into individual cells, which merge into stroma tissue developed from the reticulum of young connective tissue cells.

The area of active formation is always in the zone of invasion where osteoblasts are developed and the capillaries are in process of growth. They play no part in the penetration of the cartilage capsules; this is slowly achieved by the syncytial masses of primitive connective tissue cells (Fig. 14).

BONE GROWTH

Duhamel first demonstrated that long bones increased in length by continuous increments at their extremities, although he made no reference to the diaphyseal plates of cartilage. Dubreuil (8) has recently confirmed Duhamel's observations showing that there is no interstitial growth in the shaft of a long bone during its increase in length. In place of the ivory stylets used by Duhamel, Dubreuil employed lead pellets, periodically measuring the intervals between the pellets, radiographically. Hunter's (15) observations, with madder feeding form the foundation of our knowledge of bone growth, in that he elucidated the dual processes of deposition and absorption. He realised that cells controlled the tissue in the successive remodelling that occurs to meet growth requirements and pathological interruptions.

It has been shown that osteoblastic activity results in osseous deposits, first in the subperiosteal areas and later on the persisting cartilage trabeculae within the cartilage model. As growth proceeds, this primary bone is absorbed to form the medullary cavity. Subperiosteally, the early bone is laid down in a series of trabeculae, in lattice pattern, the intertrabecular areas containing occluded primitive connective tissue cells loosely arranged in a reticulum. This tissue is derived from the subperiosteal mesenchyme by segregation resulting from the interposition of new-formed trabeculae. Manifestations of the same growth transitions, as with the osteogenic mesenchyme elsewhere, are evinced by this tissue. Osteoblasts, osteoclasts, vessels, haemoblasts and stroma cells develop from it. Ultimately it is liberated, on the absorption of the surrounding bone, and blends with the haemogenic tissue of the medullary cavity. In later stages, these areas fill in with bone tissue which ultimately surrounds the vessels. In this way the concentric lamellae of the Haversian systems arise in the compact bone; the interstitial lamellae representing the subperiosteal deposition. Thus the whole of the shaft of a long bone is ultimately derived from subperiosteal increments.

Endochondral bone is always characterised by the presence of a nucleus of chondromucin in the centre of the trabeculae (Fig. 25). Its existence is transitory, serving to increase the stability of a bone at the site of its growth. It undergoes absorption, extending the area of the medullary cavity towards the diaphyseal cartilage.

In the epiphysis deposition is more a feature of growth than absorption, although replacement of old by new trabeculae to meet new tension and pressure stresses is a continuous process. The original mesenchymal channels form the paths finally occupied by the vessels concerned with blood supply.

It is thus seen that all the increments in bone growth are either peripheral, or terminal, whether cartilaginous or osseous in origin.

In the diaphysis the peripheral increments are entirely osseous, and the terminal increments, entirely cartilaginous. In the epiphysis, increments are solely peripheral and cartilaginous. Interstitial growth is the feature of the cartilaginous increments, whereas osseous increments are purely additive.

BONE DEPOSITION

For a long time bone has been recognised as an exceedingly active tissue, capable of considerable modifications, both by proliferation and absorption. Very little is known, however, of the nature of these processes, especially of the control of the osseous matrix, by the bone cell, both in deposition and absorption. There can be no doubt that the osteoblast is responsible for deposition and that it eventually becomes embedded in the bone substance, henceforth to be regarded as a bone corpuscle (Figs. 26 and 27). In physiological processes of absorption, osteoclasts apparently play an osteolytic rôle, at the same time they do not always appear to be essential, since bone trabeculae are frequently seen, in the process of solution, not associated with the presence of the osteoclasts.

Extensive protoplasmic ramification of the bone corpuscles, in osseous matrix, are indicated by ground sections, which display the canaliculi radiating from the lacunae. These cell processes are not revealed in ordinary preparations, the embedded bone cells resembling closely the osteoblasts, from which it might be inferred that either the protoplasmic processes are formed during the evolution of the osteoblast, or develop during the secretion of ossein. In the hope of settling this issue, preparations of developing bone were made, by fixing in Orth's fluid and staining sections with thionin blue and picric acid, according to the technique recommended by Schmorl (27). The interesting point about this method is that only the bone corpuscles actually embedded and those osteoblasts in the process of bone deposition, are typically stained. Ossein is stained a purplish green, the bone cells show a dark nucleus and pink cytoplasm. The protoplasmic processes are seen as fine filaments radiating from the cell body, forming a network of fibrils, which anastomose with similar processes from neighbouring bone corpuscles. They resemble the dendritic processes of a nerve cell, except that radiation occurs from every aspect of the cell body.

Ossein lies in the interstices of the processes.

An osteoblast in the act of secretion shows only processes radiating from the surface of the cell in relation to the trabeculae of bone substance. The ossein makes its appearance in the intervals between the processes (Figs. 28, 29). From these appearances it would seem that the secretion of ossein is carried out by the cell processes, which pass out from the cell body. It is unusual to find a bone corpuscle embedded flush with the chondromucin trabeculae, although osteoblasts are observed closely approximated, before bone deposition occurs. This implies a movement of the cell body away from the original site of deposition, a movement which might easily be associated with the development of the cell processes. It is further evident that the area of deposition is determined by the extent of the ramifications.

Von Disse (6) came to the conclusion that the protoplasm of the osteoblasts was transformed directly into bone substance, whilst Maximow (24) is of the

opinion that it is secreted directly by the cell body. Neither of these observers has accounted for the formation of the protoplasmic processes which fill the canaliculi. The occurrence of the processes only in relation to the secretion of ossein appears to be conclusive evidence that they govern the secretion which is here regarded as an exoplasm of the protoplasmic ramifications.

That the two processes of ossein and lime salt deposition are independent, is evidenced by such conditions as rickets and osteomalacia. Whether they are synchronous is another matter. Young bone can be cut without decalcification, indicating a smaller lime salt content than older bone, but this does not indicate that lime salt deposition is a secondary process to the secretion of ossein. Denby (4) has shown in the formation of spicules in sponges, that colloidal silicon is secreted as an exoplasm by the scleroblasts. It is very probable that calcium salts in a colloidal state are similarly secreted by the bone corpuscles and absorbed by the ossein.

Bast (2), by a technique of his own, has demonstrated the inter-communications between bone corpuscles by means of protoplasmic strands. He also claims that division by amitosis is a function of bone corpuscles. No evidence had been found to support this observation, which implies in osseous tissue, the power of interstitial growth; a difficult process to conceive in virtue of the hardness and inelasticity of the tissue, and a point of view which is neither supported histologically nor experimentally.

SUMMARY

Chondrogenesis and osteogenesis are growth manifestations of multipotent primitive connective tissue. The cells which engender these two processes have the same developmental origin, evincing activities which diverge as growth proceeds.

Cartilage formation precedes and is independent of osteogenesis, occurring by an ontogenetic development of the primitive connective tissue cells, the essential change in which is the appearance of a chondromucin matrix, as an exoplasm.

Bone formation is initiated by a later growth impulse of a different order. It consolidates the growth registered by the cartilage, thereby fulfilling its ultimate aim; the development of an entirely new structure, the secondary nature of which is apparent, both phylogenetically and ontogenetically.

The primitive connective tissue cells of the chondrogenetic areas in the course of growth form the chondroblasts of cartilage, the fibroblasts of the perichondrium or periosteum, the osteoblasts and osteoclasts of osseous tissue, and the haemoblasts and reticular cells of marrow. They persist and extend by growth. When the cartilage model is completed they occupy a position between it and the perichondrium. It is in this region that the osteoblasts, concerned with circumferential growth of the diaphysis, are evolved.

Invasion of the cartilage model takes place by proliferation of young connective tissue cells, the movement of the tissue occurring as a growth extension.

In the diaphysis, they rapidly form a zone of syncytial tissue which continually replaces the dead hypertrophic cells at the ossification line. This zone is the site of formation of the endochondral osteoblasts and osteoclasts, the endothelial cells of the growing capillaries, and the primitive blood cells, "the haemoblasts."

In the epiphysis, the primitive connective tissue cells grow into the cartilage mass, along channels which develop by solution of the chondromucin. When the cartilage of the epiphysis prepares itself for osseous replacement, the undifferentiated connective tissue, which has made its way to the site of the cartilage activity, proceeds as in the diaphysis with the development of osteoblasts *in situ*.

Osteoblasts are specialised cells which evolve only by the ontogenetic development of primitive connective tissue cells. They develop in accordance with growth requirements, at or near the site of their activity from pre-existing tissue, whether they engage in subperiosteal or endochondral bone disposition. In whatever situation they arise, the stem cell is the same and the transition process identical.

Osteoblasts undergo a cytomorphosis during the deposition of ossein and form branched cells, which become embedded in the bone substance. The branched cells are the bone corpuscles. Bone substance is secreted by the processes which pass out from every aspect of the cell body and anastomose with similar processes from neighbouring cells. The amount of ossein secreted by a bone corpuscle depends upon the extent of the ramification of the branched protoplasmic processes.

Osteoclasts arise at the ossification line, and subperiosteally, by fusion of the primitive connective cells. They are osteolytic in function. Disintegration occurs either by structural degeneration or by splitting up into single cells which mingle with the young connective tissue elements of the reticular tissue.

Growth in length of the diaphysis of a long bone is entirely effected by cartilage increments. Growth in diameter is achieved only by osseous increments.

Epiphyseal growth is achieved solely by the interstitial expansion of the cartilage.

Periosteum and perichondrium are one and the same structure developed from the peripheral primitive connective tissue cells of the chondrogenetic area. It is a fibrous tissue membrane; the fibroblasts are finally differentiated and show no tendency to revert to undifferentiated connective tissue cells. In no way associated with bone deposition, it affords an attachment for neighbouring structures, and serves as a "limiting" membrane for osteoblastic activity.

APPENDIX I

No opportunity has presented itself for consulting the original papers of Duhamel, Haller and Hunter. The references to these authors were obtained from the text of Keith's work, *Menders of the Maimed.*

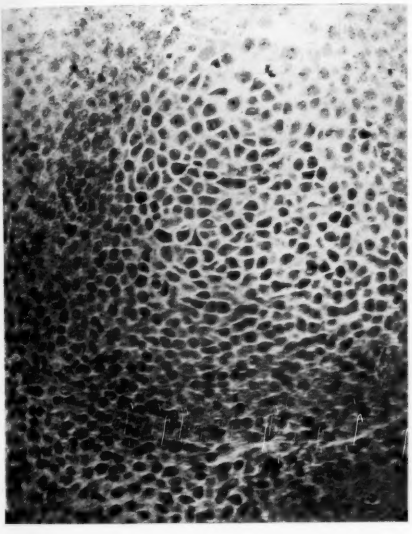
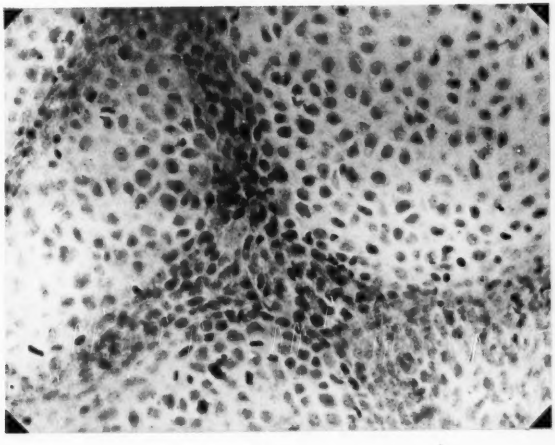


Fig. 1



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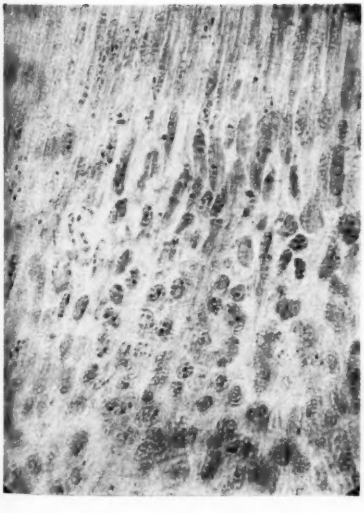

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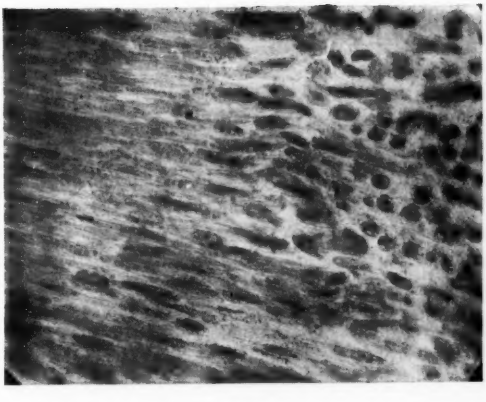

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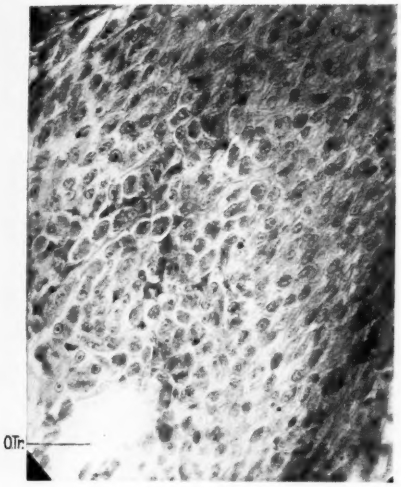

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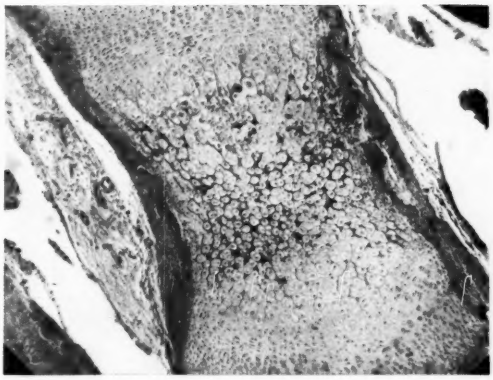

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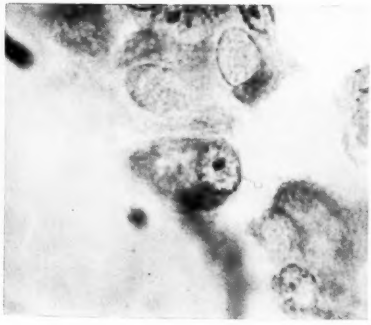

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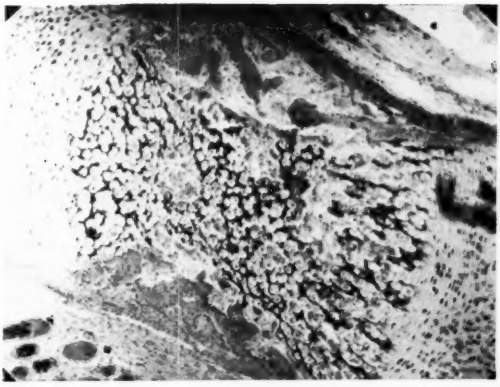

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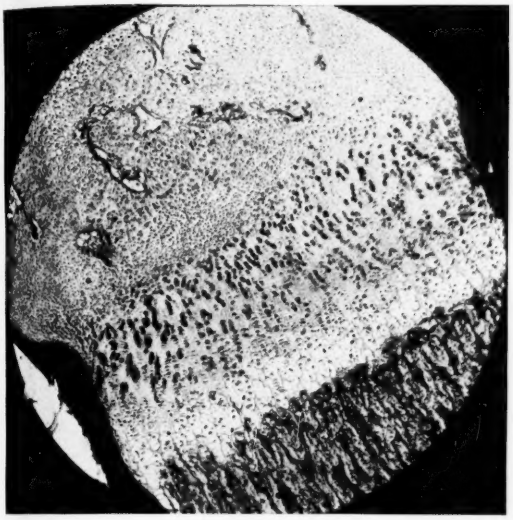

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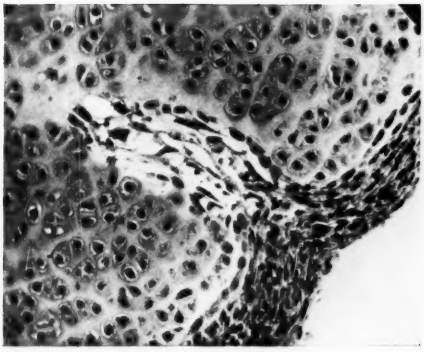
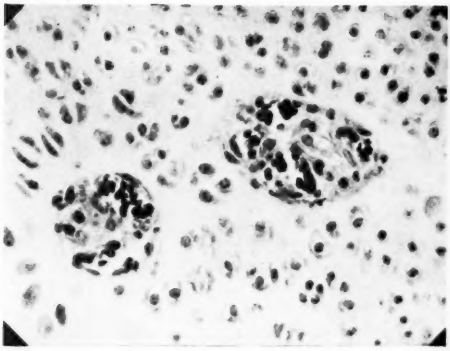


Fig. 10

Fig. 11



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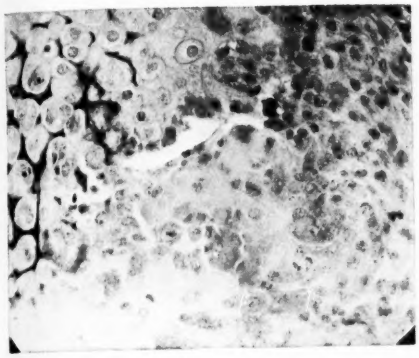

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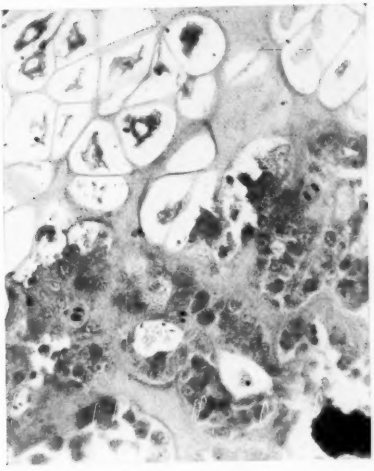

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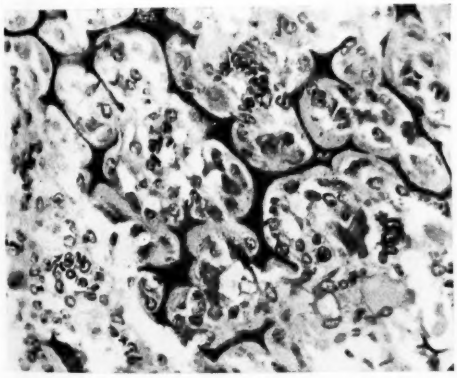

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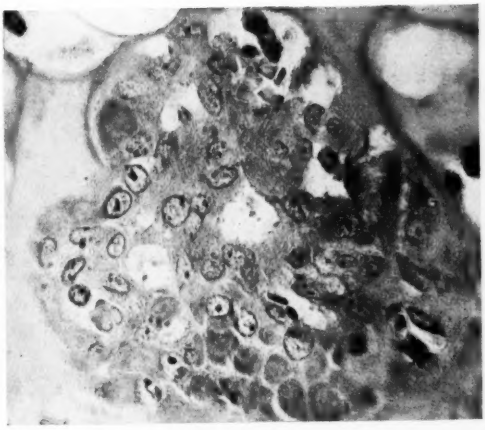
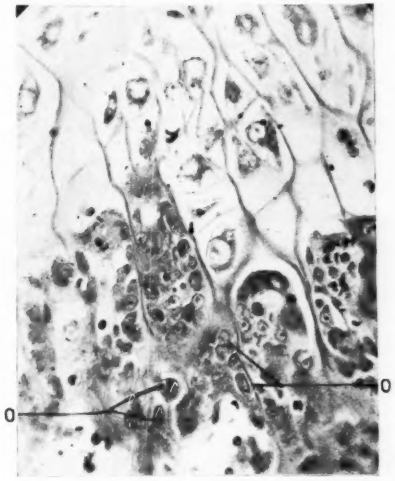


Fig. 16

Fig. 17



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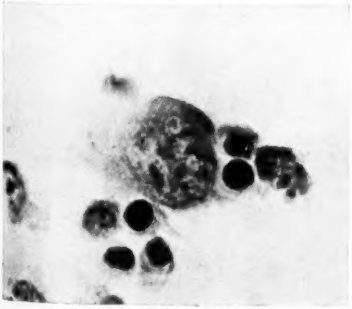

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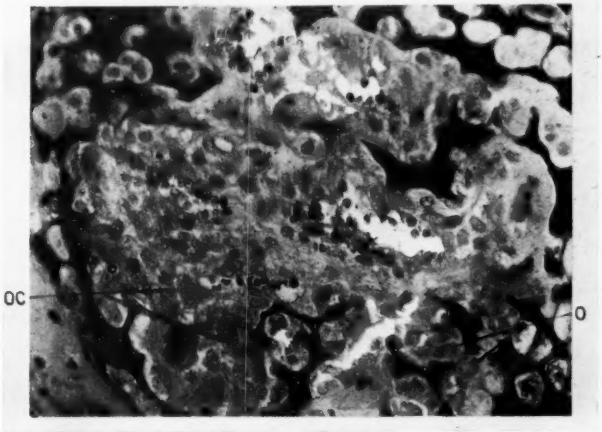
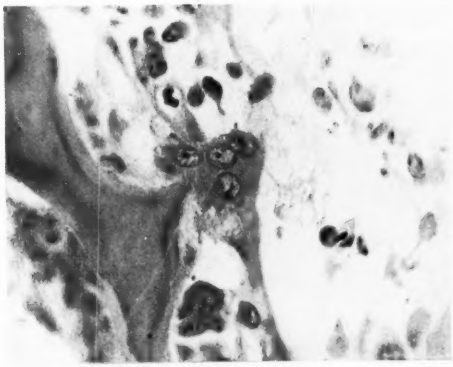


Fig. 20

Fig. 21

Fig. 22



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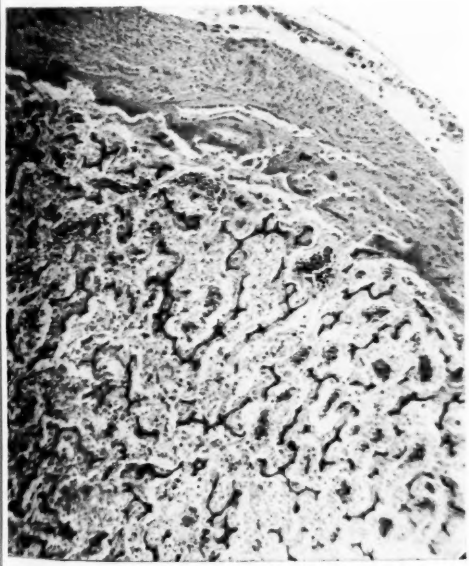
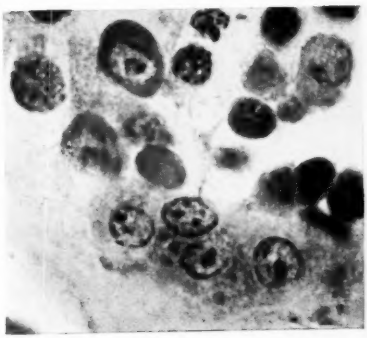


Fig. 25

STUMP—The Histogenesis of Bone



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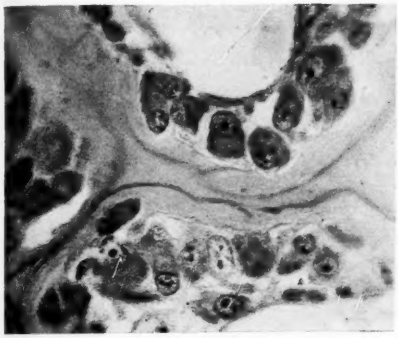

Fig. 26

Fig. 27

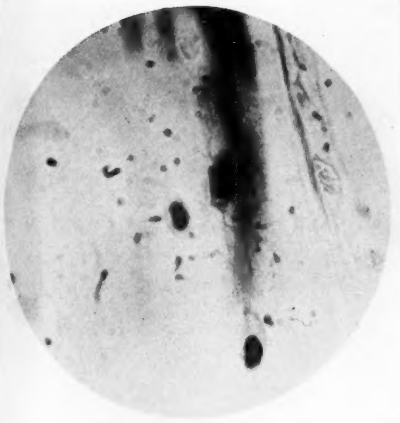

Fig. 28

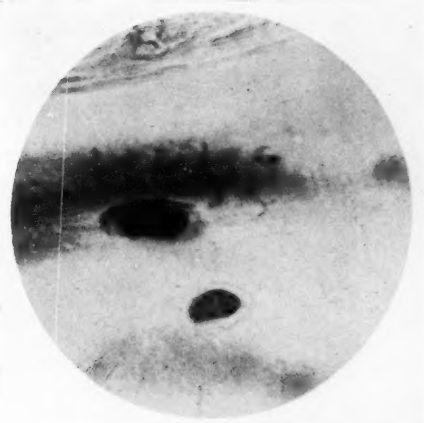

Fig. 29

APPENDIX II

MacEwen has introduced the term "diaphyseal" to replace the current term "epiphyseal," used to denote the plate of cartilage that separates the diaphysis from the epiphysis during the growing period. He aptly remarks that: "the activity of the cartilage is related to the diaphysis and not to the epiphysis."

DESCRIPTION OF PLATES

PLATE I

Fig. 1. Cartilage formation.
Fig. 2. Cleavage of the mesenchyme in the formation of a joint cavity.
Fig. 3. Formation of fibroblasts from mesenchyme cells.
Fig. 4. Tangential section of the periosteum showing the subperiosteal mesenchyme.

PLATE II

Fig. 5. Loosening of the cells of the subperiosteal mesenchyme in the formation of osteoblasts. (*O.Tr.*) subperiosteal bone.
Fig. 6. Early endochondral ossification showing calcified cartilage trabeculae, subperiosteal bone with the gaps through which the mesenchymal invasion penetrates, and areas of young connective tissue within the cartilage model.
Fig. 7. An osteoblast partially embedded, showing the eccentric nucleus and large attraction sphere. ×1166.
Fig. 8. Early endochondral ossification, showing the subperiosteal bone and the arrangement of the cartilage trabeculae.

PLATE III

Fig. 9. Showing the ordered arrangement of the cartilage at the diaphysial plate (serial zone and hypertrophic zone), the ossification line and scattered groups of hypertrophic cartilage cells around the mesenchymal channels in the epiphysis.
Fig. 10. Subperichondral mesenchyme invading the cartilage.
Fig. 11. The liberation of cartilage cells in a mesenchymal channel.
Fig. 12. Undifferentiated connective tissue cells and capillaries in the mesenchymal channels of the epiphysis.

PLATE IV

Fig. 13. Subperiosteal mesenchyme invading the diaphysis of the cartilage model.
Fig. 14. Syncytial masses of undifferentiated connective tissue cells, irrupting cartilage capsules at the ossification line.
Fig. 15. The deposition of ossein on calcified chondromucin trabeculae.
Fig. 16. Formation of capillary lumina.

PLATE V

Fig. 17. Differentiation of primitive connective tissue cells, showing osteoblasts, endothelial cells and a haemoblast (central cell).
Fig. 18. Formation of osteoblasts (*O*) at the ossification line.
Fig. 19. A young megakaryocyte.
Fig. 20. The formation of osteoclasts (*OC*) in early endochondral ossification. (*O*) osteoblasts.

PLATE VI

Fig. 21. A young osteoclast at the ossification line.
Fig. 22. An osteoclast surmounting a bony spicule.
Fig. 23. An osteoclast.
Fig. 24. An osteoclast showing the characteristic grouping of the nuclei.
Fig. 25. Chondromucin in trabeculae.

PLATE VII

Fig. 26. Osteoblasts.
Fig. 27. Embedded osteoblasts, the attraction sphere is visible in many of them.
Fig. 28. Protoplasmic processes radiating from an osteoblast.
Fig. 29. Protoplasmic processes radiating from an osteoblast.

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NOTES ON THE ANATOMY OF THE LIVING EYE, AS REVEALED BY THE GULLSTRAND SLITLAMP

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The ready accessibility of the eye to observation and the great clinical importance of a knowledge of its structure led, from the earliest times, to a vast amount of research on the subject of its anatomy. We find, if we consider the steps by which our present views have been arrived at, that each successive stage of increased knowledge has been preceded by the discovery of some more perfect means of investigation. While investigators had to rely on painstaking dissection alone, the minute structure of the tissues necessarily remained unknown, though one is constantly surprised at the remarkably detailed and accurate results which were arrived at by this means. With the introduction of the microscope a fresh impetus to the study of the eye was apparent, and it was not long before the microscopic slide yielded confirmation or denial of existing views and made possible a hitherto unguessed minuteness of description. Yet even the most perfect microscopes and the best histological technique have failed to elucidate entirely the structure of such delicate tissues as are found in the eye. Post-mortem change alone may be responsible for much distortion of the picture, while the coagulants employed in the necessary fixation may produce artefacts which are very difficult to interpret. For example, the existence of a hyaloid membrane has often been discussed. The older anatomists demonstrated it by dissection, but the histologists have often failed completely to find it, while they have also disagreed considerably as to the structure of the vitreous which it enclosed. Again, although the sutures of the lens can be demonstrated by maceration methods, it is well-nigh impossible to study their arrangement in a microscopic section. With still greater force does this apply to pathological conditions in the lens.

The discovery by Babbage in 1847 of the ophthalmoscope marked yet another stage in our advancing knowledge, since it provided a means of checking, by examination of the living eye, those conclusions which had been arrived at by post-mortem dissection and sectioning. The great value of the ophthalmoscope lay in the power it conferred of examining the deeper parts of the eye, magnified and in their natural colours. Yet even the ophthalmoscope could not reveal the structure of the living vitreous or lens, save in grossly pathological cases.

It remained for Henker in 1911, by the inspired combination of the

Gullstrand slitlamp and the binocular corneal microscope, to inaugurate yet another epoch in ophthalmological research and to supply at once a method of investigation of value to the clinician for the early diagnosis of disease, and to the anatomist both for the confirmation of existing knowledge and for the elucidation of many of the remaining riddles of ophthalmic structure. By means of Gullstrand's apparatus it is now possible to obtain an "optical section" of the living eye, i.e. to illuminate against a dark background an exceedingly thin slice of the transparent media of the eye and to observe the surface of such a section stereoscopically at magnifications ranging from × 9 to × 103. In this way many new and important anatomical facts have come to light, especially in connection with the structure of the lens and vitreous, while at the same time the clinician is now able to examine, in the living patient, structures (such as the individual endothelial cells on Descemet's membrane) which had hitherto been demonstrated to him by the histologist only.

It is proposed to give a brief account of the anatomy of the normal living eye as seen with the slitlamp. (A short description only of the method of examination follows. Fuller details of this, together with the findings in pathological conditions, can naturally be found in the clinical journals and text-books on the subject. Many of the diagrams are after Prof. Vogt, whose *Atlas* on the subject contains invaluable information.)

THE APPARATUS

This consists of:

(*a*) The Gullstrand slitlamp, an apparatus comprising a Nernst or a nitra lamp, a focussing lens (condenser), a narrow slit, the width of which can be reduced to 40 μ, and an illuminating lens by means of which the uniformly illuminated image of the slit is accurately focussed on to the desired portion of the eye.

(*b*) The Zeiss-Czapski binocular corneal microscope (lenses giving magnifications of × 23 and × 40 are the most useful) mounted upright so as to allow of the examination of the illuminated area of the eye. The whole examination must be carried out in an absolutely dark room and for the observation of fine details the observer must be well dark-adapted.

METHODS OF EXAMINATION

The narrow beam of light from the slitlamp may be utilised in a variety of ways. The most usual way is to use a fairly wide slit (say 1 mm.) and by accurate focussing to illuminate a section of the cornea 1 mm. thick. This section has a prismatic form and the various surfaces presented by it can be seen in fig. 1 (*a*). In the normal cornea the superficial surface *a* and the proximal face of the section *b* can be most easily examined. Structures (such as nerve fibres) in the substance of the cornea can be localised by moving the beam and noting at what depth in *b* they first light up. It can easily

be seen from fig. 1 (*a*) and (*b*) that by narrowing the slit of the lamp the illuminated slice of cornea can be thinned correspondingly until it assumes the proportions of a thick microscopic section, the surfaces *a* and *b* being reduced almost to lines. (If a micro-arc lamp is used instead of a nitra lamp a section only 20μ thick can be obtained.) This is the method of "optical section." It can be applied with great success to the cornea and lens. Fig. 2 shows diagrammatically the path of the beam of light through cornea, lens and vitreous

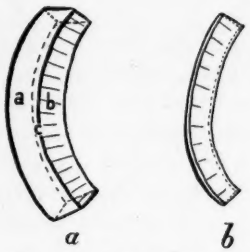

Fig. 1 (*a*) Diagram of corneal prism: *a* = anterior surface, *b* = proximal face of section, *c* = posterior surface seen through *a*.
(*b*) Diagram showing effect on corneal prism of narrowing the slit.

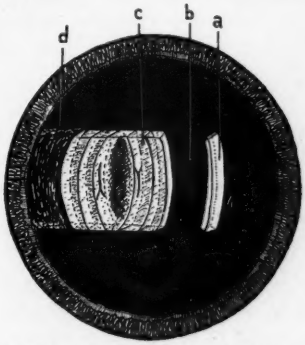

Fig. 2. The path of the beam through an eye with dilated pupil: *a* = corneal prism, *b* = anterior chamber, *c* = lens, *d* = vitreous.

in an eye with widely dilated pupil. It will be noted that two brightly illuminated areas appear at *a* and *c*, corresponding with the path of the beam through cornea and lens respectively[1], separated by a dark (optically empty) space which represents the anterior chamber *b*, while behind the lens the vitreous is faintly fluorescent, *d*.

Two other methods of examination must be briefly described:

(*a*) The method of retro-illumination, in which, with an undilated pupil, the beam is thrown on the iris and the scattered light reflected from this is used to examine the posterior surface of the cornea, the angle of the anterior chamber, and the blood vessels at the limbus. This method is especially useful for showing the circulation of the blood and the physiological bedewing of the corneal epithelium.

(*b*) The examination of reflecting surfaces. In this method the microscope is focussed on the area of specular reflection of one or other of the reflecting surfaces (e.g. anterior and posterior surfaces of cornea, anterior surface of lens, etc.). By this means very fine details, such as the individual endothelial cells on Descemet's membrane, can be seen.

[1] The term "fluorescence" is applied to the property of certain transparent tissues of emitting a glow where the beam passes through them. Thus, the cornea is fluorescent but the aqueous humour is not.

After this brief résumé of the technique, the appearances of the normal living human eye will be dealt with and certain points of anatomical interest, which have been brought out by the method, described. In many cases the findings have only served to confirm those of the anatomist and the histologist (e.g. the presence of nerves in the superficial 2/3 of the cornea only), while in others (e.g. the zones of discontinuity in the lens) they may be said to have very materially improved our conception of the condition.

THE CONJUNCTIVA

(*a*) The ocular conjunctiva.

(*b*) The limbal region.

(*a*) The vessels can be very well observed, arterioles, venules, capillaries and lymphatics being distinguishable. The lymphatic sheaths are best marked on the veins; they were first described by Koeppe, who also found them on small arteries. Occasionally they may be seen quite apart from any blood vessel. They are easiest of observation in old people, since a physiological

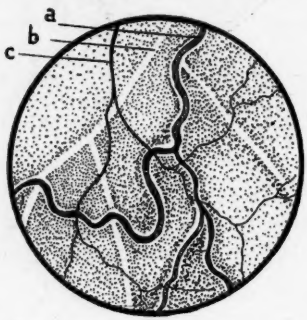

Fig. 3. Conjunctiva in old age: *a*=vein with lymphatic sheath, *b*=lymphatic, *c*=arteriole.

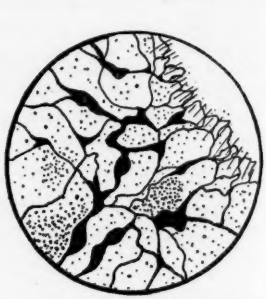

Fig. 4. Varicosities of the conjunctival vessels. (The limbus is on the upper right-hand side.)

senile deposit of haematogenous pigment takes place in the superficial conjunctival tissues, stopping short at lymphatic or other vessels, so that these show up clearly. Fig. 3 shows a portion of conjunctiva with such pigmentation. It is not at all uncommon to find localised varicosities of the conjunctival vessels (fig. 4).

(*b*) The limbal region. It is in the region of the limbus that the slitlamp shows up detail extremely well, since it is here possible to examine the conjunctiva by retro-illumination. In the first place the circulation of the blood can be observed. In the larger vessels the blood column may appear broken into segments, while in the capillaries the passage of the individual corpuscles can often be watched. Venules and arterioles have very little to distinguish them, but the direction of the blood flow will always make the distinction

certain. The small capillary loops at the limbus are usually empty of blood and may therefore be mistaken for lymphatics, but it is only necessary to massage the eye through the lid to cause them to fill rapidly. If an individual capillary loop is examined it will be seen that the direction of the blood flow within it is not constant as in the veins and arteries, but that there is a certain amount of oscillation and intermittency, the direction of the blood current changing from time to time and the loop occasionally becoming quite empty. The speed of the corpuscles in the capillaries has been estimated as 1·6–3·5 mm. per second and the diameter of the vessels in which the movement is best seen is ·01–·03 mm. (Koby).

In many people, but not with equal distinctness in all, an arrangement of the limbal vessels known as "palisades" can be seen. In these cases the vasa afferentia of the capillary plexus run in slightly elevated, radially arranged, folds of conjunctiva. The vessels are straight, show no lateral branches and are superficial to the veins. As age advances the palisades become whiter and more dense in appearance and some of the vessels may become invisible. The final row of capillary arcades also becomes impervious in age. Fig. 5 shows the arrangement of the limbal vessels and the differentiation into a more central zone of capillary loops and a more peripheral zone of "palisades" (vasa afferentia) and venules. While examining the limbus one often sees nerves entering the cornea. These have a definite medullary sheath which extends about 0·5 mm. into the cornea. Some individuals show nerve fibres in far greater numbers than others.

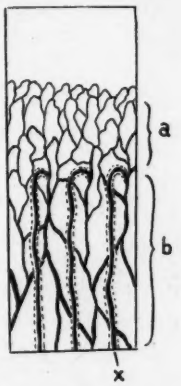

Fig. 5. The limbal region of the conjunctiva: *a* = zone of capillary loops, *b* = zone of palisades, *x* = vessel in palisade (modified from Vogt).

THE CORNEA

One is surprised at first by the amount of fluorescence of the cornea. When seen by the ordinary methods of examination it appears almost perfectly translucent and "optically empty," but when illuminated by the slitlamp beam it glows with a greyish mottled light and appears very far from homogeneous. The surface epithelium is, in the central part, perfectly smooth and polished in appearance. The individual cells cannot be seen, but on its surface are minute particles (mucus, shed cells, etc.) which slide about as the eye is moved. Nearer the periphery the surface becomes less smooth and an appearance, which is usually described as "bedewing," is seen. In this region under good conditions the bedewing can be seen to be composed of minute droplets, each probably corresponding to an epithelial cell. Vogt thinks the appearance is due to an increased saturation of the peripheral epithelium with nutrient fluid from the capillary plexus and also to slight irregularities of surface caused by the vascular loops. The peripheral bedewing is constant and normal: in pathological conditions it may extend to the central area.

The substance of the cornea presents a mottled or speckled appearance through which the corneal nerves run like fine silk threads. They are invariably found in the superficial 2/3 of the cornea and they branch dichotomously at an angle of 60° (rarely trichotomously) and end superficially in the epithelium. At their points of branching are often knob-like thickenings.

THE POSTERIOR SURFACE OF THE CORNEA

The slitlamp has made it possible for the first time to observe the living individual cell and by focussing on the posterior reflecting zone of the cornea every endothelial cell on Descemet's membrane can be seen distinctly. The appearance is of an olive-yellow shining surface covered with small, slightly convex, hexagonal dots. Each dot appears quite separate from the rest. With a low power this gives the appearance of a fine yellow mosaic, but with higher powers, especially in the pig's eye, the hexagonal form of the cells and a dark dot in the centre of each can be made out. The central dark dot is not the nucleus itself, which is colourless, but is a small shadow caused by its prominence in the thin scale-like cell. The endothelium is not quite smooth but shows, especially in the periphery, a wavy irregularity. In old age the hexagonal patterning becomes less distinct and regular, and round dark patches appear in places. (These are the proliferations of the endothelium described as wart-like projections into the anterior chamber by Hassal and Henle.) Fig. 6 shows the endothelium in youth and old age.

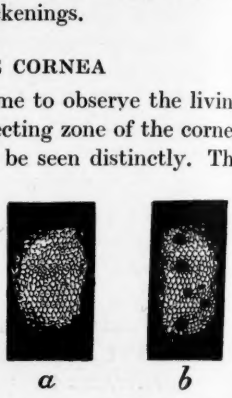

Fig. 6. Corneal endothelium: *a* = in youth, *b* = in old age. The dark spots are Hassal-Henlé bodies.

THE LENS

It is perhaps in the examination of the lens that the slitlamp has revealed most that is new and interesting. The lens fibres do not lend themselves well to fixing and embedding so that microscopical examination is rarely satisfactory, while maceration methods, though they reveal the so-called "suture lines," fail altogether to show the structure of the capsule or to indicate the existence of the optical "zones of discontinuity." The lens is not optically homogeneous. It was long ago described as possessing a central nucleus, the curvature and index of refraction of which differed considerably from those of the superficial or cortical part. That the lens was constantly altering in density and optical properties throughout life was also well known, but never before was it possible to examine the living lens, noting at each examination the number and depth of the zones of discontinuity (i.e. those zones between which a difference in refractive index exists), examining in detail not only the surface of the capsule but also the surface of each of these zones or nuclei (for the slitlamp has taught us that the lens of the text-books with its single nucleus and its cortex is a thing of the past), observing the suturing of each

layer and noting with actual measurements the changes in structure, in thickness, in optical properties, of each layer throughout life.

It must be realised that, as seen with the slitlamp, the lens consists of the capsule, the cortical portion, the adult nucleus, and two embryonic nuclei, an outer and an inner. Each of these layers has a different index of refraction and is more or less sharply demarcated from the adjacent layers, so that the surface of each layer acts as a convex or concave mirror as the case may be, and gives rise to reflecting areas and zones of discontinuity in the same way as do the anterior and posterior surfaces of the cornea (or as does any line of contact between two transparent media of different refractive index). The reflecting areas are really bright in four regions only, namely, the anterior and posterior surfaces of the lens and the anterior and posterior surfaces of

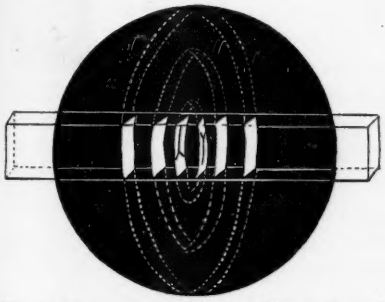

Fig. 7. The passage of the broad beam through the lens (from Vogt).

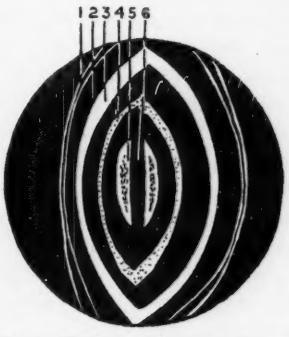

Fig. 8. The lens with narrow beam illumination: 1 = capsule and reduplication line, 2 = cortex, 3 = adult nucleus, 4 = outer embryonic nucleus, 5 = inner embryonic nucleus, 6 = central dark area.

the adult nucleus. The zones of discontinuity, however, can be easily seen in the other situations as well.

The fluorescence of the lens is even greater than that of the cornea and seen with a broad beam it presents a pale greenish-grey colouration, becoming more yellow towards the posterior pole. Fig. 7 shows diagrammatically the various zones of the lens as seen with the broad beam. If the beam is narrowed until the surfaces become linear, the appearance is that shown in fig. 8. We can therefore say that passing from the anterior surface backwards, the beam of light traverses the following layers:

1. The anterior capsule. With a narrow beam this shows as a thin bright line. Immediately under it is a second bright line (the reduplication line) separated from it by a dark interval which is slightly wider at the equator than at the poles. This represents the surface of the cortex.

2. The cortex. This is not seen before the tenth year and becomes progressively thicker throughout life.

3. The adult nucleus.

4. The outer embryonic nucleus.

5. The inner embryonic nucleus. This is like a plano-convex lens, the plane surface being turned towards

6. The central dark portion.

7, 8, 9, 10, 11 and 12 similarly in reverse order back to the posterior capsule. See figs. 7 and 8.

By focussing the microscope on the reflecting zone of the anterior capsule one sees an appearance which has been named "the lens shagreen." The surface does not appear perfectly smooth but is covered with little elevations and depressions somewhat reminiscent of pigskin leather. These do not correspond in size with the epithelial cells, but are much larger, so that the

Fig. 9. The lens shagreen.

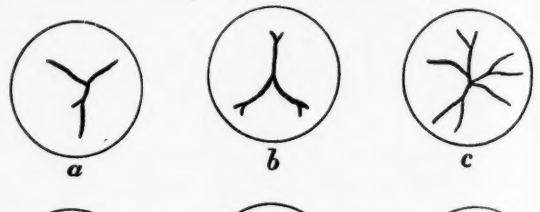

Fig. 10. Suturing of lens: a = anterior embryonic nucleus, b = posterior embryonic nucleus, c = outer embryonic nucleus, d = adult nucleus, e = cortex, f = another common form of adult nucleus (after Vogt).

appearance is not comparable with the mosaic pattern made by the corneal endothelium. In young subjects under suitable conditions small dots can be made out just under the surface of the shagreen, which are the individual epithelial cells. Fig. 9 is an attempt to represent the appearance, which is, however, difficult to portray without the use of colour and tone. Immediately under the capsule lies the cortex. The surface of this shows suturing, usually of a branching star-shape, but very variable. It must be understood that in all the layers the suturing becomes easier to see as age advances and that in very few lenses can the sutures on each of the surfaces be seen with equal distinctness. In early youth usually only the anterior and posterior embryonic Y-sutures can be seen and of these the posterior is the more obvious.

The surface of the adult nucleus presents a suture which consists either of

a branching star or of a vertical line bifurcating at each extremity. That of the outer embryonic nucleus is a simple star.

The suture on the anterior inner embryonic nucleus is in the form of an *upright* Y, not, as so often stated, an inverted Y. Between the two plano-convex embryonic nuclei there is a narrow dark space and in 25 per cent. of all individuals this contains, just deep to the anterior Y, a few dot-like opacities (anterior embryonic cataract of Vogt).

Deep to the central dark space one comes on the posterior inner embryonic nucleus with its *inverted* Y-suture, usually easily seen and showing branching of its lower limbs, and so passes through the other layers in inverse order until the posterior capsule is reached. Some typical forms of the various sutures are shown in fig. 10. The posterior capsule presents many points of interest. It gives a very bright reflection and by focussing on the reflecting zone one can see the lens shagreen as in front, but the patterning appears much smaller, possibly owing to the fact that the reflecting surface is concave instead of convex. Naturally no epithelial cells are seen here.

If one finds the posterior Y-suture and then follows down the nasal limb of this to its bifurcation and examines the posterior capsule at this point, one sees a white line forming a segment of a small circle (hence called the "arc line") or more rarely a complete circle; from the centre or lower part of this circle a wavy corkscrew-like white thread can be seen hanging down behind the lens. This arc line and thread-like body are embryonic remains. The arc line represents the opened-out anterior end of Cloquet's canal and the filamentous body the anterior end of the hyaloid artery. That Cloquet's canal is a real structure and remains patent in adult life has been shown by clinical observations on cases of retinal disease with superficial pigment formation, in which free pigment granules in course of time passed forwards along Cloquet's canal and appeared on the posterior capsule of the lens within the limits of the arc line, but nowhere else.

These embryonic remnants (minimal persistent hyaloid) can be found, according to Vogt, in all individuals if carefully looked for. It is of great interest to note that they occur, not at the posterior pole where they would cause interference with central vision, but downwards and to the nasal side of this. The exact form and extent of them are variable. Fig. 11 shows two common types.

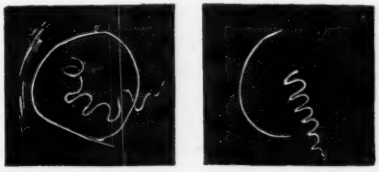

Fig. 11. Arc line and hyaloid remnant (Vogt).

Comparatively often the slitlamp will reveal other traces of the vascular capsule of the lens in the form of dark lines and superficial opacities, but these are not sufficiently common to be considered normal though they occur far more often than was originally thought.

Immediately behind the lens is a dark (optically empty) narrow space,

the retro-lental space. The size of this space apparently varies with the type of light used, the brighter the light (e.g. arc light) the narrower the space. This seems to indicate that the retro-lental space is not truly optically empty, but is filled with a more delicate scaffolding than is the vitreous proper.

The structure of the vitreous has always been a subject for controversy, and the slitlamp cannot be said to have entirely settled the matter, though it has opened the way for further investigations. It seems, however, to suggest the existence of the retro-lental space and of a membrane (the much discussed hyaloid membrane) separating the vitreous from this. The hyaloid membrane is not smooth and tense, but appears like a thin, greyish, structureless curtain hanging loosely down behind the lens. It is thrown into vertical folds, and waves slightly as the patient moves his eye. Some observers (Vogt) state that this hyaloid membrane is not present with equal distinctness in all eyes. It appears to be a membrane formed by the apposition of lamellae and may be denser in some cases than others. Koeppe has confirmed its existence and that of the retro-lental space with the slitlamp and Fuchs has demonstrated it anatomically.

Behind this membrane is seen the vitreous. Here individual variation is great and the limits of the normal seem scarcely to have yet been defined. In the majority of cases one sees waving membraneous films with strands and threads here and there. Fine dots or gross fibres appear to be pathological. The normal vitreous is by no means optically empty and contains more cellular and filamentary structures than was previously thought. There does not seem to be a definite lamellar structure or any canals, but further research is needed. The opacities seen appear to have about the same specific gravity as the intervening jelly, since they move on movements of the eye but always return to rest at the same place.

The retina is not accessible to examination with the slitlamp under ordinary conditions.

THE IRIS

Here one gets an extremely beautiful stereoscopic view in great detail. The crypts, the region of the circulus arteriosus iridis minor, the fibres of the sphincter pupillae (in blue eyes) and the pigment border of the pupil are extraordinarily well seen. These points have, however, already been more or less thoroughly studied and very few new facts seem likely to come to light since it is (in normal cases) only the surface of the iris that can be examined and not a true section as in the case of the cornea, lens and vitreous. One point worthy of passing note is the extreme frequency with which remains of the pupillary membrane can be discovered with the slitlamp. These are present in a large percentage of otherwise normal eyes, and are fine threads which pass from the region of the minor circle either to adjacent points on the circle or across the pupil, being either free or attached to the iris, more rarely the lens.

To sum up we can state that the introduction of the slitlamp method of

examination has opened a way to a more exact conception of the anatomy of the living eye. Further research is badly wanted, but already one can say that the lamp has done much to correct and check opinions founded on dissection and microscopic examination alone. Especially useful is the improved knowledge of the structure of the lens. The shagreening of the anterior capsule, the arrangement of the sutures, the persistence of the hyaloid remnant, the changes in thickness of the various layers throughout life are subjects which have been very little stressed up to the present. Soon they will become matters within the experience of the average medical student. It is so important for the anatomist to check the results of the dissecting room by an appeal to the living body, and so seldom is it practicable or possible, that this improvement in our methods of observation merits more at the hands of scientists than to be considered merely the ornament of an ophthalmic consulting room.

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A full bibliography is given in Vogt's *Atlas,* which should be consulted in the first instance.

THE ANATOMY OF RUDIMENTARY FIRST THORACIC RIBS WITH SPECIAL REFERENCE TO THE ARRANGEMENT OF THE BRACHIAL PLEXUS

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INTRODUCTION

From a consideration of anatomical and surgical literature first thoracic ribs are a rare condition compared with "cervical ribs"—Fischel of Prague (1) reported that in routine necropsy examination covering a period of four years, "cervical rib" was found in one per cent. of all bodies examined. I can find only six cases of rudimentary first thoracic ribs recorded by observers in Britain. The associated arrangements of the soft parts may give rise to symptoms, and this has made the study of "cervical ribs" one of practical interest to the clinician. It is only recently that the importance of these anomalies from the neurological point of view has been fully recognised—Bramwell and Dykes (2) cited numerous cases of "cervical ribs," but none in which the first thoracic rib was rudimentary. This may have been due partly to the faulty technique of an X-ray examination. Unless the vertebrae are counted from the Atlas downwards, it is difficult to decide whether or not a rudimentary first is a cervical rib or a first thoracic rib, and it is possible that the latter is more common than literature would lead us to believe. A description of the arrangement of the soft parts in conditions where the first thoracic rib is rudimentary may be of value in explaining certain symptoms, in cases where an abnormal rib is suspected.

RÉSUMÉ OF THE LITERATURE OF RUDIMENTARY FIRST THORACIC RIBS

In the year 1744 M. Hunauld communicated to the Royal Academy of Sciences, Amsterdam (3) a memoir on variations in the number of ribs. He figured a portion of the skeleton of an adult "in which the first rib on each side, well formed posteriorly and articulated with the first dorsal vertebra, became blended with the second rib, which was by this union much larger than usual." Sandifort (4) has figured "costa prima dextra hominis adulti, quae duo plane distincta capita habet" in which a like arrangement was present.

In a memoir on cervical ribs, Knox (5) directed attention to Hunauld's and Sandifort's cases, and described some specimens in his own collection. He was of opinion that the specimens represented by Hunauld and Sandifort were analogous to one which he figured, and he considered each specimen to

be an example of the blending of a cervical rib with the first true or thoracic rib.

Knox recorded a specimen where the shafts of two adjacent left ribs were intimately blended together so as to form a broad bone. At the vertebral end it was deeply cleft and presented two heads, necks and tubercles; and at the sternal end it was bifid, and possessed two distinct costal cartilages. He considered that this was a case of cervical rib, which though blended with the first true rib, yet possessed a distinct sternal connection, but in the absence of a knowledge of the requisite details respecting its sternal and vertebral connections, he stated that "it may be a partial fusion of the first and second thoracic ribs." Turner (6) in 1870 gave a description of two examples of "two-headed ribs in man." These were dried specimens he found in the Anatomical Museum of the University of Edinburgh. He came to the conclusion that "the upper rib element is a cervical rib and that it has fused with the first dorsal rib." He was of opinion that the specimens figured and described by Knox and Hunauld were examples of the same condition.

In 1883 Turner (7) contributed a lengthy paper on "Bicipital Ribs in Man." Although he had been familiar with specimens of this kind in the Anatomical Museum of the University of Edinburgh, the two cases he described were the first examples he had met with in the dissected subject during his thirty years' experience as a teacher of anatomy. He made accurate and complete observations of vertebrae, ribs, sternum, muscles and arteries, but in connection with the nerve arrangement he mentioned merely that "the first dorsal nerve occupied the short cleft between the necks of the two ribs prior to their fusion." He came to the conclusion that these were undoubtedly cases in which the bicipital character of the upper rib was due to fusion of the shafts of the first and second thoracic ribs a short distance in front of their tubercles.

The knowledge which Turner gained from these cases led him to reconsider his conclusions, regarding the cases which he described in 1870. At that time he had recognised that the two fused ribs closely resembled a first and second thoracic rib but by attaching importance to the characters of the vertebrae, he erroneously described them as a fusion of a cervical with a first dorsal. In his paper in 1883 he decided that the specimens described by himself in 1870 were examples of fusion of first and second thoracic ribs, and not a fusion of a cervical rib and a first dorsal rib. He placed a similar interpretation on Sandifort's and Knox's cases and he said that "we must accept M. Hunauld's own statement of the nature of his specimens as correct, and discard the view of its being a cervical rib blended with a first thoracic, which was suggested by Dr Knox."

In 1874 Struthers (9) published an account of "an imperfect condition of the first pair of ribs," but as the vertebrae and soft parts were incomplete he was not certain that they were not supernumerary cervical ribs. In a footnote to this paper he stated that in the skeleton of a three-toed sloth (*Bradypus tridactylus*) the first thoracic rib was rudimentary. Among the lower animals

Bradley (10) found a rudimentary first thoracic rib in a horse. Its appearance was similar to that found in man, but no observations were made in detail of the arrangement of the other parts.

Bellamy (11) in 1874 described a subject where the first ribs were rudimentary. They were 1½ inches long and each resembled a small horn attached to the first thoracic vertebra. The subject had six lumbar vertebrae. He mentioned that the first thoracic nerve lay on the anterior surface of this rib but gave no further detail with reference to the brachial plexus.

Lane (12) in 1885 described a case where there were present seven cervical vertebrae, thirteen rib bearing vertebrae, five lumbar and five sacral. The head of the first rib articulated with the side of the body of the eighth vertebra. A dense fibrous band extended from the extremity of the rib to the upper margin of the rib below it. He stated that "the greater part of the ninth nerve crossed the neck of the rib, and just before doing so it was joined by a large branch from the tenth spinal nerve." He regarded rudimentary first thoracic as cervical ribs holding that there was in such cases an extra vertebra intercalated in the cervical series. The arrangement of nerves in itself was sufficient, I think, to prove that Lane was not justified in this assumption. Macphail (13) in 1903 demonstrated a case of rudimentary first thoracic ribs. He found that there was an irregular block of partly ossified cartilage at the side of the upper part of the manubrium sterni. This was part of the first arch. He did not find any fibrous band passing forwards to this bar of ossified cartilage from the tip of the rib. Macphail found the cords of the brachial plexus "normal on both sides" as regards contributory nerves. The lower cord lay immediately behind the subclavian artery on the right side while the corresponding cord on the left side was displaced upwards by the projecting extremity of the first rib, and was separated by it to some extent from the artery.

In 1895 Hertslet and Keith (14) found a rudimentary first thoracic rib in a Magyar. They gave a comparative table of the arrangement of soft parts in this subject, and in one presenting cervical ribs. In the case of the former they merely stated that "the second thoracic nerve goes to the first intercostal space and gives a branch to the first thoracic nerve."

In 1902 Dukes and Owen (15) published a case of rudimentary first thoracic ribs with a note on the lower part of the plexus. They stated that "the greater part of the second thoracic nerve enters the brachial plexus by joining the first thoracic nerve about 2·5 cm. external to the latter's exit from the intervertebral foramen. To effect this junction it has to pass over the second rib joining the first thoracic nerve at the inner side of the ligamentous portion of the first rib. The combined trunk then proceeds outwards over the ligamentous portion of the first rib, closely applied to and below the trunk of the eighth cervical nerve."

Wilfred Harris (16) dissected thirty bodies in order to examine carefully the motor distribution of the brachial plexus. He found that the plexus was either prefixed or postfixed. In the former the contribution from the fourth

cervical nerve was large, and in the latter small, but he did not make any remarks on the condition of the ribs in these two different types of plexus.

In 1914 Lucas (17) published a paper on two cases of cervical ribs, with observations on the state of the brachial and lumbar plexuses. She found a certain amount of prefixation of the brachial plexus in one of her cases, and with prefixation of the lumbar plexus there was diminution or absence of the twelfth rib.

Wood Jones in 1910 (18) offered a new explanation of these anomalous conditions of the upper part of the thoracic operculum. In his lengthy paper on "The relation of the limb plexuses to ribs and vertebral column," he asserted that the commonly called subclavian groove on the normal first rib was not due to the subclavian artery, but to the pressure of the eighth cervical nerve and the first thoracic nerve in the lowest cord of the brachial plexus. He described an "atypical" form of first thoracic rib in which the anterior part and the posterior part were flattened in one plane, and sharply divided from one another by a gutter running downwards and backwards in which the lowest trunk of the brachial plexus was situated.

In conditions where the first thoracic rib was ligamentous the same observer asserted that the ligamentous part of the rib commenced at the site of the nerve groove, and the nerve cord and subclavian artery lay on the ligament (as will be seen later this is not what is found in my specimens). His explanation of the "atypical" variety of first rib was that it was due to the second thoracic nerve causing an extra downward strain upon the first rib at the point of crossing. He considered that in rudimentary first thoracic ribs this strain and pressure were greater because of the inclusion of the greater part of the second thoracic nerve in the plexus. He was of opinion that in cases of rudimentary first thoracic ribs the nerve cord cut the bony rib short, and passed outwards on the ligamentous part of it. Wood Jones had no opportunity of dissecting such a rib in relation to surrounding structures. He based his explanation upon the description given by Dukes and Owen (see above). He considered that the diagram given in Hertslet and Keith's case supported his view, although these observers stated merely that "the tenth nerve goes to the first intercostal space and gives a branch to the ninth." He found support from Lane who stated that "the greater part of the ninth nerve crossed the neck of the rib, and just before doing so it was joined by a large branch from the tenth spinal nerve."

Macphail was an exception for he said, "the cords of the brachial plexus are normal on both sides as regards contributory nerves."

Turner in his case of bicipital ribs stated that "the first dorsal nerve occupied the short cleft between the necks of the two ribs prior to their fusion," and that "the brachial nerves rested in a groove on the inner border and upper surface of the shaft of the conjoined ribs." While my own dissections reveal a large contribution from the second thoracic nerve, the combined trunk in them does not pass over the ligamentous part of the rib, and therefore they do not support the explanation offered by Wood Jones.

In support of his view that the development of the ribs was dependent on that of the nerve, Wood Jones called attention to the eleventh and twelfth ribs. He pointed out that the downward slope of the eleventh and twelfth nerves was greater than that of the corresponding ribs, and that the eleventh nerve left the shelter of the eleventh rib and cut across the tip of the twelfth rib, and he offered the suggestion that the false ribs were abbreviated by the nerves being pulled downwards across the somites in which the ribs took origin. He found from his dissections that the length of the twelfth rib was dependent on the obliquity of the eleventh intercostal nerve, and in cases in which the twelfth rib was a mere rudiment the eleventh nerve took a much more oblique course downwards. From these observations Wood Jones concluded that the gathering together of the nerves into the plexus for the supply of the arm was the factor which determined the normal limitation of the ribs to the special segments posterior to the seventh cervical segment. In other words the cervical vertebrae did not carry ribs because the plexiform arrangements of the nerves running to the fore limb did not permit of their development. He thought that the reason for the absence of the ribs in the lumbar region was that the nerves from these segments were gathered together into the plexus for the supply of the hind limbs. In limbless snakes all the vertebrae had ribs, and he considered that the completeness of the rib series was due to the absence of a nerve plexus.

Professor Mouchet (20) disagreed with Wood Jones about the groove on the first rib. His investigation took the form of:

(1) Examination of ribs in the dry state.
(2) Dissections.
(3) Frozen sections.

His conclusions were that the interscalenic groove on the first rib corresponded to the passage of the subclavian artery and that the groove was due to the contact with the vessel, but he added (1) that at the back of the vascular groove there existed a nervous groove due to the passage of the nerve trunk formed by the eighth cervical and first thoracic nerves, (2) that in a case where the scalenus minimus was well developed the artery was separated from the bone by a fibrous plane due to the extension of the muscle tendon. He said: "Wood Jones does not state how many subjects he examined and he thinks in the lying position of the subject the artery is lifted off the rib." Mouchet did his dissections with the subject in the sitting position.

In order to substantiate his arguments Wood Jones (21) estimated the bulk of the various nerves in the lower part of the brachial plexus with fine electrician's wire. He made them into nerve cords which were fixed by being dipped into melted solder. He examined forty ribs and plexuses, and concluded that the greater the contribution from the first thoracic nerve to the plexus the deeper the sulcus upon the first rib. He found that when the whole of the first thoracic nerve passed over the rib a downward bend was produced in the rib at this point. He found also that in the cases where the groove was divided into two, it was occupied, not as Mouchet showed, by the subclavian

artery and lowest trunk, but by the eighth cervical nerve and the first thoracic nerve respectively.

Wingate Todd (22) examined five subjects to ascertain the relationship between the first rib on the one hand and the subclavian artery and first thoracic nerve on the other. He used a strong solution of formalin in preparing his subjects whereas Wood Jones used carbolic acid and half the quantity of formalin as a preservative. The nerves and vessels were thus more fixed in position. In four of the ten dissections Wingate Todd found that the lowest nerve cord of the brachial plexus did not touch the rib. As regards the markings on the first rib Todd's observations corroborated the findings of Mouchet. He examined the nerve groove in several cases, and found its depth was greater in proportion to the increased obliquity of the first rib from the horizontal and it was also dependent on the distance between the middle line of the body and the medial border of the first rib.

In 1912 Wingate Todd (23) published a description of a specimen of rudimentary first thoracic rib, but the subject was an "old and badly preserved one and it was not possible to make exact observations." It was possible, however, to ascertain that the majority of the fibres of the second thoracic nerve joined the plexus. It also supplied the spaces between the rudimentary rib and first complete rib and the space between the first complete and second ribs.

DESCRIPTION OF FOUR SPECIMENS OF RUDIMENTARY FIRST THORACIC RIBS. (Figs. 1 and 2)

Subject A (Fig. 1).

Adult Male: Bilateral Rudimentary First Thoracic Ribs

Parts well preserved

Condition of Bones.

Vertebral column. Normal number of vertebrae, viz., seven cervical non-rib bearing, twelve thoracic rib bearing, five lumbar non-rib bearing, sacrum (five pieces fused).

Ribs. Twelve pairs. First rib, *left side* (Fig. 1) consisted of three parts: (*a*) proximal osseous part, (*b*) intermediate ligamentous, (*c*) distal osseous.

(*a*) *Proximal part* $2\frac{1}{2}$ inches long. The head articulated with the side of the upper part of the body of the first thoracic vertebra, and the tubercle articulated with the transverse process of the same vertebra. There was a deep gutter on the upper surface near the tip of the shaft. It passed laterally and forwards and lodged the combined trunk of the first thoracic and second thoracic nerves. Behind this and on the upper surface of the rib there was a faint groove caused by the eighth cervical nerve. (*b*) *Ligamentous part* in the form of a band three inches long and $\frac{1}{4}$ inch in width passed from the tip of the shaft to the edge of the sterno clavicular joint and to the distal osseous part. (*c*) *Distal osseous part* was very small and in the form of a projection from the upper and lateral angle of the manubrium sterni.

The right first rib presented the same three parts. (*a*) *The proximal osseous*

part (3¼ inches) was slightly longer than on the left side. It presented a head, a neck, a tubercle and a shaft. Near the anterior part of the upper surface of the shaft there was a narrow well defined groove which passed forwards from its medial to its lateral side, and in this groove the combined trunk of the first thoracic and second thoracic nerves was situated. (*b*) *The ligamentous part* (2¼ inches long) was shorter than on the left side. It passed from the tip of the shaft to the distal osseous portion. (*c*) *The distal part of this rib* in the form of an incompletely ossified bar of cartilage (1 inch long) was fused with the cartilage of the second rib which was ossified. The eleventh and twelfth ribs on each side were longer than normal, the last rib being 5½ inches long on the right side, 4 inches long on the left.

The scalenus anterior muscle (right side). Origin normal. Insertion three fold. (1) Anteriorly by a membranous band 1⅛ inches long into the medial half of the ligamentous part of the rib. (2) Into the medial side of the shaft of the rib, really the medial lip of the groove which lodged the lowest trunk of the plexus. (3) The lateral lip of the groove by a narrower and smaller insertion. (The lowest trunk of the plexus therefore passed through the muscle.)

The scalenus medius muscle (right side). Origin normal. Insertion into the lateral aspect of the shaft of the first rib near its tip, then fused with the external intercostal muscle, and continued into the middle of the upper surface of the second rib.

The subclavian artery (left side, Fig. 1). (The apex of the left lung was 3¼ inches above the tip of the rib.)

Origin from the arch of the aorta. It did not present the usual convexity upwards, but crossed over the lung 1½ inches below its apex. A band of fascia fixed to the pleura above and below the artery crossed and compressed the vessel, and in addition it was covered by the anterior insertion of the scalenus anterior muscle. The artery had thus a tendency to make an S-shaped bend. The third part of the artery crossed the ligamentous part of the first rib, 1 inch beyond the tip of the shaft of the rib, and continued laterally lying on the second rib.

Branches normal.

Right side. Origin from the innominate. It presented the same constriction and bend and crossed the ligamentous part of the first rib just beyond the tip of the shaft and continued laterally over the second rib.

Cervical plexus normal.

Brachial plexus, formed by C 4, C 5, C 6, C 7, C 8, T 1, T 2, the contribution from the second thoracic nerve was very large on both sides. It passed upwards over the second rib and joined the first thoracic nerve at the medial border of the shaft of the first rib ¾ of an inch external to the intervertebral foramen, and the combined trunk passed forwards and laterally and lay in the groove already described on the upper surface of the shaft of the first rib.

The anterior divisions of C 5, C 6, C 7 and partly C 8, united to form the outer cord of the plexus which lay in front of the third part of the axillary

artery. It pierced the coraco brachialis muscle, and divided into musculo cutaneous and outer head of the median, the latter joined the inner head of the median about the middle of the upper arm.

The posterior divisions of C 5, C 6, C 7, C 8 were joined by a very slender branch from the first and second thoracic nerves and formed the posterior cord. The greater part of the first and second thoracic nerves (which formed a combined trunk) passed below the first part of the axillary artery and divided into two branches one of which contributed to form the ulnar, the other joined the greater part of the eighth cervical nerve and formed the inner head of the median.

The eighth cervical nerve mainly passed in front of the second part of the axillary artery and most of it formed the inner head of the median, but it gave off a slip which united with the first thoracic nerve and the second thoracic nerve and formed the ulnar.

The branches given off by the radial (three in number) to the triceps came off higher than usual at the level of the lower border of the pectoralis minor. The nerves to the subscapularis and teres major came off the axillary nerve. The medial cutaneous nerve of the forearm was given off by the combined trunk T 1, T 2, 1½ inches above its bifurcation. The posterior primary divisions C 2, C 3, C 4, C 5, C 6, C 7, C 8 were all found, the eighth cervical nerve was above the rudimentary rib.

SUBJECT B (FIG. 2). BILATERAL RUDIMENTARY FIRST THORACIC RIBS.

Vertebral Column. Seven cervical non-rib bearing; twelve thoracic rib bearing; remainder not available for description

Ribs. The first rib, *left side*, consisted of three parts. (*a*) *A proximal osseous part* 2½ inches long, presented a head, a neck, a tubercle and a shaft, with a faint groove which commenced on its medial side, and passed over its upper surface. This groove was caused by the combined trunk of the first and second thoracic nerves. There was also a faint groove on the upper surface of the shaft caused by the eighth cervical nerve. (*b*) *A fibrous expansion* not so definite as on right side. (*c*) *A distal osseous part* fused with upper lateral angle of manubrium sterni.

Right side. (*a*) *A proximal osseous part* was 3¼ inches long and consisted of a head, a neck, a tubercle and a shaft. There was a well developed deep broad groove on the upper surface and near the tip of the shaft. The groove passed forwards and laterally and contained the combined trunk of the first and second thoracic nerves. The medial lip of the groove was raised and formed a sharp spine into which the scalenus anterior muscle was inserted. (*b*) *A ligamentous part* 1¾ inches long was in the form of a fibrous band which passed from the anterior extremity of the rib to a distal osseous part. (*c*) *A distal osseous part* was fused with the upper and lateral angle of the manubriun sterni and with the cartilage of the second rib.

The scalenus anterior muscle had two heads of insertion and the subclavian

artery passed between them. *The anterior head* was inserted into the ligamentous part of the rib. *The posterior head* (a scalenus minimus) was inserted into the medial lip of the groove near the tip of the shaft of the rib behind the artery, and immediately in front of the common stem of the first and second thoracic nerves.

The scalenus medius muscle was inserted into the lateral and upper surface of the shaft of the rib from the tubercle behind for at least 2 inches anteriorly.

The subclavius muscle. Origin by a narrow pointed tendon attached to the fibrous part of the first rib. *The external intercostal muscle* was attached above to the osseous and fibrous parts of the rudimentary rib, below to the upper border of the second rib.

The left subclavian artery passed laterally between the two insertions of the scalenus anterior muscle and lay on the ligamentous part of the rib.

The left vertebral artery entered the transverse process of the seventh cervical vertebra.

The right vertebral artery entered the transverse process of the fifth cervical vertebra.

Cervical plexus normal.

Brachial plexus. C 4, C 5, C 6, C 7, C 8, T 1, T 2 on both sides. The eighth cervical nerve lay along the upper surface of the rudimentary rib for $1\frac{3}{4}$ inches of its length, and grooved the neck and upper surface of its shaft. The first and second thoracic nerves joined together at the medial border of the shaft of the rib about its middle, and as a common stem passed over the medial and upper surface of the rib and lay in the groove already described. The common stem of the first and second thoracic nerves joined the eighth cervical nerve a short distance lateral to the lateral border of the first rib and formed the lowest trunk of the brachial plexus. The fifth and sixth cervical nerves formed the upper trunk. The seventh cervical nerve formed the middle trunk. Subdivision of trunks normal.

Nerve supply of second intercostal space. On the right side the second thoracic nerve gave the large contribution to the first thoracic nerve already described. In addition it had a branch which passed along the under surface of the second rib for two inches where it bifurcated: (*a*) into a branch which passed up to supply the first intercostal space; (*b*) a branch which passed forwards and supplied the second intercostal space.

3, 4, 5, 6, 7, 8, 9, 10, 11, 12, intercostal and subcostal nerves normal.

COMMENTS

In connection with this abnormality the following points arise for discussion:

A. *The contribution from the second thoracic nerve*

Lane mentioned a large contribution from the second thoracic nerve.

Dukes and Owen noted that the greater part of the second thoracic nerve

entered the plexus, and the combined trunk (T 1, T 2) lay on the ligamentous part of the rib.

Hertslet and Keith pointed out that "the 10th (second thoracic) gave a branch to the 9th (first thoracic)."

Wingate Todd said the majority of the fibres of the 10th nerve (second dorsal) joined the plexus, but his specimen was an "old and badly preserved one and it was not possible to make exact observations."

Macphail found the cords of the brachial plexus normal on both sides as regards contributing nerves.

Turner made no mention of the second thoracic nerve.

In each of my four cases there was a very definite and large contribution from the second thoracic nerve and that was perhaps the most outstanding feature.

My specimens supported the view of Wood Jones that rudimentary first thoracic ribs were associated with a postfixed type of plexus, but not entirely so, as all the four specimens which I have dissected showed a contribution from the fourth cervical nerve. Lane, and Dukes and Owen, were previously the only observers who definitely observed postfixation of the plexus.

B. *The grooving of the rib*

In my specimens each rib was deeply grooved by the combined trunk of the first and second thoracic nerves, so much so that the nerve lay as it were embedded in the rib substance. The direction of the groove was slightly forwards and laterally. Macphail's notes gave one the impression that the nerve rested on bony rib. Turner stated that "the brachial nerves rested in a groove on the inner border and upper surface of the shaft of the conjoined ribs," but in Dukes and Owen's case the nerve lay on the ligamentous part of the rib. Wood Jones considered that the nerve trunk cut the bony rib short and expected it to rest on the ligamentous part of the rib.

(In the figures the nerve has been lifted out of the groove.)

C. *What is the primary factor in the etiology of rudimentary first thoracic ribs?*

Wood Jones considered that it was due to the extra strain caused by the inclusion of the second thoracic nerve in the lowest trunk of the brachial plexus. He said that "the ligamentous part of the rib commences at the site of the nerve groove, and the nerve cord and subclavian artery lie on the ligament." While my specimens supported the fact that the second thoracic nerve is a large contributor in these cases, they did not corroborate the view that the ligamentous part of the rib commenced at the site of the nerve groove, as in all my cases the nerve cord rested on bony, not ligamentous tissue, and indeed there was bony tissue beyond the groove, in which the nerve was situated. Hertslet and Keith's diagram did not show that the nerve crossed over the ligamentous part of the rib, and Macphail led one to the conclusion that the

nerve rested on the rib. Lane also said that "lying on the back of the left first rib is a nerve formed by the greater part of the ninth and part of the tenth." These reports I think show that the crossing of the nerve did not always occur at the commencement of the ligamentous part of the rib. Mouchet (20) and Wingate Todd (22) have also shown that the extent of pressure due to the "nerve trunk" is very variable and not nearly so powerful a factor in grooving a rib as Wood Jones considered.

Further, the size of the rib was not in direct ratio to the size of the nerve trunk, because on the left side of subject *A* the contribution from the second thoracic nerve was smaller than on the right side yet the left rib was smaller than the right one. The same was found in subject *B*, i.e., there was no direct ratio between the size of the contribution from the second thoracic nerve and that of the rib. If the nerves alone were responsible, one would not expect to find bony tissue developed beyond the line of crossing. If they caused atrophy and disappearance of the ribs, there would not have been even a ligamentous part of the rib. Yet both bone and ligament were found beyond the line of crossing in my four specimens. From these observations it is reasonable to conclude that the disposition of the nerve trunks alone is insufficient to account for the presence and length of rudimentary first thoracic ribs.

D. *Relationship between the anatomical arrangement of the soft parts and clinical signs and symptoms in cases of "abnormal first ribs"*

Symptoms have been due to nerve compression of the lowest trunk of the brachial plexus where the first thoracic rib was normal in size and shape. This was first pointed out by Bramwell and Dykes (2) in 1903. Stafford and Telford (24) in 1920 fully recorded and discussed seven examples of this nature. They expressed the opinion that a "predisposing cause seems to be the anatomical relation of the nerve trunk and the rib, when the bone is bevelled by a trunk which receives a large contribution from the upper two dorsal roots." In consideration of the fact that so many examples of "cervical ribs" have been reported in anatomical literature, it is truly remarkably how totally this by no means uncommon source, of serious nervous troubles, has been ignored. Thus Keen (25) stated: "I had never seen a case of recognised cervical rib until October 1905." Lewis Jones reviewed in 1908 a group of cases to which he had drawn attention in 1893 under the title of "Symmetrical Atrophy of the Hands of Young People," and found that a well marked cervical rib existed in no fewer than ten out of fourteen patients of the group. Conditions which were given such diagnostic labels as brachial neuritis, brachial neuralgia, uniradicular palsy, progressive muscular atrophy, writer's cramp, symmetrical atrophy of the hands constituted a group of not inconsiderable size, and we know now that the symptoms were due in most cases to the presence of a cervical rib. According to Thorborn (26) when a cervical rib was present its shape and direction were more important than its size. He considered that

when the rib passed laterally it avoided vessels and nerves and thus did not produce symptoms other than deformity. He also mentioned that the mobility of the rib was important. If it was free anteriorly, movement occurred at its vertebral end, and symptoms arose more readily than if it was fixed in front forming a complete arch. During inspiration the rib rises at the rate of 16 inspirations per minute. An upward excursion of the rib occurs almost 1000 times per hour, or about 23,000 times a day. This slight upward pressure continued for years may have a deleterious effect and cause stretching of the nerves passing over it. In cases of cervical rib the eighth cervical and first thoracic nerves form a trunk which passes over the surface of the cervical rib. If the trunk is lodged in a gutter in the rib-substance such as has been observed in the specimens of rudimentary first thoracic rib which I have described, the effect will be felt much more if the limb is forcibly extended or subjected to strain. The presence of a groove embedding the nerve, as it were, should be reckoned as a factor in the causation of symptoms. I do not intend to discuss all the symptoms due to a cervical rib, but being under the impression that rudimentary first thoracic ribs may have, on some occasions, escaped observation, I have considered the clinical reports of a few cases of cervical rib with a certain amount of scepticism. Anaesthesia of part of the hand and forearm is well known to be a common symptom of cervical rib. Case 6 of Bramwell and Dykes (2) showed sensory disturbance extending 3 or 4 inches above the elbow joint, on the medial (inner) side, a fact which suggested that the second thoracic nerve was involved, and as this nerve was not likely to be affected in a case of cervical rib, the condition may have been one of rudimentary first thoracic rib. Thorborn (26) gave a picture of the "painful areas" in a patient of his, with a cervical rib. The region affected included the inner (medial) side of the arm as far up as the axilla as if there had been involvement of the second thoracic nerve.

Keen (25) reported that in one of his patients a diagnosis was made of a cervical rib, but the supposition was proved by the skiagraph to be incorrect. The condition was found to be a rudimentary first dorsal rib. This was the only instance which I found where the abnormality had been observed by a surgeon, and unfortunately there were not any definite notes made of the symptoms and signs. It is also well known that the swelling at the root of the neck in certain cases of cervical rib has been mistaken for an aneurism. Indeed in some cases at operation, the artery has been found to be markedly dilated. But the curious fact is, that in these cases the dilatation of the vessel was lateral or distal to the point where the artery passed over the cervical rib, and distal to the point where it passed behind the scalenous anterior muscle, i.e. really distal to the point of pressure.

Murphy made a special point that in the inspiration movements of the thorax, the artery was caught between the rib and the scalenous anterior and he thus explained the aneurism. Even granting, as is probable, that the artery was pinched between the muscle and the bone at this point, this obstacle

to the circulation should have produced a dilatation proximal to the point of constriction and not distal. Keen made a careful study in his case and observed the small calibre of the vessel up to the point at which the artery emerged from behind the scalenous anterior, and its calibre was nearly doubled from there down to the brachial. In my dissections of rudimentary first thoracic rib the calibre of the subclavian artery as it lay behind the scalenous anterior was much reduced. This was due to the presence of a tough band of fascia which passed from the pleura above and below the vessel and compressed it (see Fig. 1). As the artery did not cross the osseous part of the rib there could not have been any compression from contact with it.

In conclusion it is a pleasure to express my gratitude to Professor Waterston for his kindness in giving me the opportunity of fully examining and describing these specimens.

SUMMARY

The large contribution from the second thoracic nerve has been observed in all four dissections.

The disposition of the nerve plexus alone is not the only factor which causes the abnormality.

From a consideration of the symptoms and signs of cases recorded as "cervical ribs," I am of opinion that in a few, the condition has been one of rudimentary first thoracic rib.

DESCRIPTION OF PLATE

FIG. 1. Subject A. A dissection of the left side of the neck showing a rudimentary first thoracic rib.

1. Transverse cervical artery.
2. Inferior thyroid artery.
3. Vertebral artery.
4. Common carotid artery.
5. Scalenus anterior muscle.
6. Internal mammary artery.
7. Left innominate vein.
8. Ligamentous part of first rib.
9. Vertebral artery.
10. Eighth cervical nerve.
11. Combined trunk of 1st and 2nd thoracic nerves.
12. Stellate ganglion.
13. Second thoracic nerve.
14. Rudimentary first thoracic rib.
15. Apex of left lung.
16. Band of fascia
17. Second rib.
18. Subclavian artery.

FIG. 2. Subject B. An anterior view of a dissection of the neck, showing bilateral rudimentary first thoracic ribs.

1. Right rudimentary first thoracic rib, proximal osseous portion.
2. First thoracic nerve.
3. Second thoracic nerve.
4. Head of left first rib.
5. First thoracic nerve.
6. Second thoracic nerve.
7. Tip of proximal osseous part of first rib.
8. Scalenus anterior muscle.
9. External intercostal muscle.
10. Tendon of subclavius muscle.

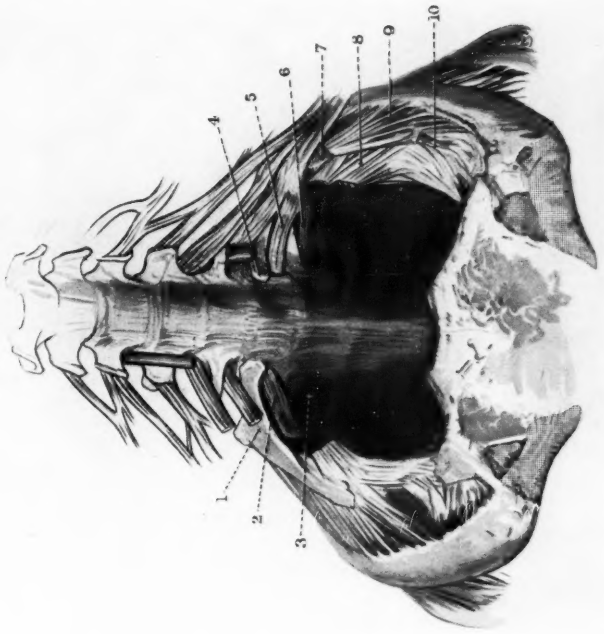

Fig. 2

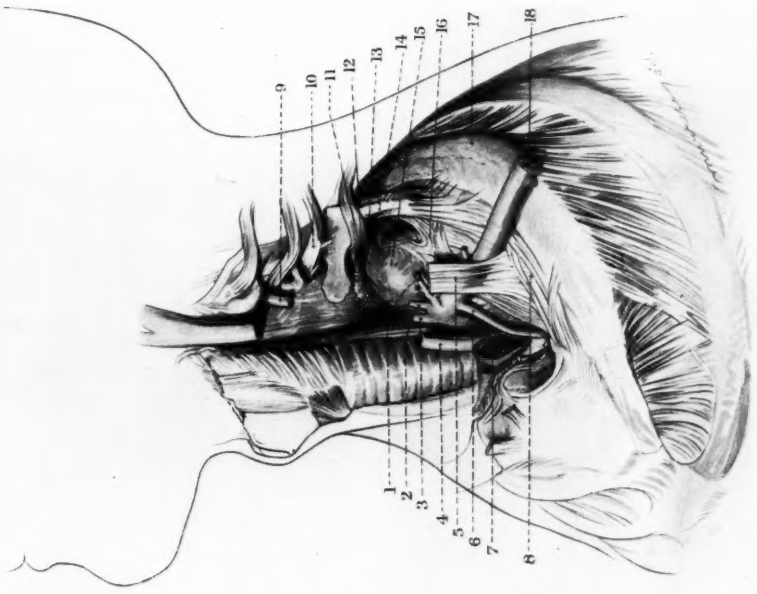

Fig. 1

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THE NATURE OF MUMMIFICATION AND MACERATION ILLUSTRATED BY THE MALE WHITE SKULL

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INTRODUCTION

In a recent publication I have discussed the shrinkage in linear dimensions of the cranium consequent upon drying after maceration (1). From that study I concluded that there is no material difference in shrinkage to be observed in male or female, White or Negro skulls. Certain questions presented themselves during that investigation, questions which had not been foreseen at the beginning of the research and therefore could not be answered by that study itself. In consequence I have felt it imperative to review the work and check my former results. The reasons for the present renewed study are three: first, the previous sample was a small one; secondly, the maximum shrinkage after maceration we now find to occur during the first few hours after removal from the water and not on the second or third day as Pearson asserted; thirdly, I did not check the shrinkage after maceration against the shrinkage on simple mummification.

To correct these inadequacies in the previous work I determined to take new samples, numbering approximately 50 for each sex of each Stock, White and Negro, and to submit each sample to a thorough examination. Every skull was first mummified for twelve weeks, the linear dimensions being measured weekly. Next the skull was macerated, measured wet and permitted to dry for a further period of twelve weeks, again being measured weekly. By mummification one means simply drying after stripping off all soft tissues (except those in the nose) to facilitate the process of drying. To compare properly the progress of shrinkage in mummification and after maceration it was necessary to measure each skull weekly throughout both periods of drying. It has been my intention to investigate the nature of maceration and to note what results, if any, could be attributed to maceration beyond simple dehydration of the bone.

This work has involved a long and minute analysis of the shrinkage tables

for each skull in addition to the thousands of measurements called for by the routine examination. But for the loyal and energetic co-operation of my secretary, Miss Lindala, it could never have been carried through successfully. We have now completed the survey for male White skulls, a series 49 in number. At a later date the survey of female and Negro skulls will be presented.

No attempt has been made to select skulls on the basis of age or condition of sutures, since I have already shown that shrinkage bears no relation to these characters. The sample used in this work has been kept quite separate from the former sample so that we might have the opportunity of comparing the mean values and their errors in the two groups.

SHRINKAGE IN MUMMIFICATION

In the dissecting-room there is naturally some drying out of the material although this is kept very moderate in amount by the adoption of covers to the dissecting tables in addition to the usual wrapping of the cadavera (2). The skull on removal from the dissecting-room does not therefore give a really correct measurement of its linear dimensions in the body. In consequence after the initial measurement the skull is soaked in water for twenty-four hours and then bisected, after which it is measured again while still wet. The difference between the first and second measurements gives the alteration in dimensions resulting from drying in the dissecting-room. The second measurement is used as the basis for calculation of shrinkage. Immediately after the second measurement is made the skull is placed on the drying rack where it stays for twelve weeks, being measured afresh each week. I have already mentioned that all soft tissues are stripped off from the exterior of the skull. The brain and dura are also removed before the drying commences.

Table I. *Male White crania*, 1922–23.

Number 49. Mummification.

		Mean	S.D.	C. of V.
(A)	Length, S.R.	184·32±·770	7·99 ±·544	4·33± ·295
Cleaned, wet,	Length, glab.	183·73±·759	7·88 ±·537	4·29± ·292
not macerated,	Breadth	146·39±·549	5·70 ±·388	3·90± ·266
not cut	Aur. Height	117·18±·426	4·42 ±·301	3·77± ·257
(B)	Length, S.R.	184·45±·771	8·00 ±·545	4·34± ·296
Immediately	Length, glab.	183·84±·760	7·89 ±·537	4·29± ·292
after section,	Breadth	146·31±·546	5·67 ±·386	3·92± ·267
wet	Aur. Height	117·16±·432	4·48 ±·305	3·82± ·260
(C)	Length, S.R.	183·13±·768	7·97 ±·543	4·35± ·296
Final dry	Length, glab.	182·41±·766	7·95 ±·542	4·36± ·297
dimensions	Breadth	145·43±·534	5·54 ±·377	3·81± ·260
	Aur. Height	116·28±·419	4·35 ±·296	3·74± ·255
(D)	Length, S.R.	1·34±·568	0·590±·402	44·03±3·540
Total	Length, glab.	1·40±·514	0·534±·364	38·14±2·962
shrinkage	Breadth	0·88±·620	0·643±·438	73·07±7·169
	Aur. Height	0·89±·284	0·295±·201	33·15±2·484

Table I gives the means and variabilities with their errors of the first measurement (A), the second measurement (B), the last measurement (C), and the total shrinkage (D). The differences between the means of (A) and (B) show

the changes undergone by the skulls as a result of shrinkage in the dissecting-room; for practical purposes they are negligible. It is however noteworthy that, on the average, bisection of the skull has an effect upon breadth too minute for consideration. Such difference as the saw cut makes is neutralized by the increase in breadth which results from soaking. This initial immersion in water brings about a possibly slightly greater increase in supra-orbital length than in glabellar length and has no effect upon auricular height. It is evident however that the errors in mean length render insignificant the difference in measurement.

(C) gives the final mummified dimensions. Comparison of the variabilities in this section with those of section (B) shows that there is no erratic shrinkage in the sample as a whole: this means that mummification itself introduces no unforeseen factor into cranial dimensions.

Section (D) gives the mean shrinkage with its variability in each dimension. The means are not obtained by subtraction of the figures in (C) from those in (B) but by the addition of the individual figures for shrinkage. This procedure brings about a difference in the second decimal place alone.

The coefficients of variation in section (D) show that shrinkage in supra-orbital length is but slightly more variable than shrinkage in glabellar length, which in its turn is somewhat greater than shrinkage in auricular height. Auricular height measurements whether of cranium or head (3) appear to be, of all linear cranial dimensions, the most constant and least susceptible to change by accidental or extra-cranial factors. On the other hand shrinkage is much more variable in breadth than in any other dimension. In my previous work I commented upon the change in position of the Euryon during drying. Cranial breadth is the dimension most flexible and most easily influenced. The reason for this will become evident in later studies.

The total shrinkage on mummification may conveniently be expressed as a percentage of the final mummified dimensions rather than as a percentage of the original green dimensions, since in its practical application shrinkage will usually be calculated upon the mummified skull for obvious reasons. The figures are:

Supra-orbital length	0·73 %
Glabellar length	0·77 %
Euryon breadth	0·60 %
Auricular height	0·76 %

Hence mummification results in a fairly definite and uniform shrinkage of between 0·7 and 0·8 per cent., and this amount added to the final mummified dimension will give a pretty close approximation to the figure for the green cranium.

Shrinkage in breadth is appreciably less than in the other dimensions. This seems to be due to failure of the squamous temporal bone to follow closely the retraction of the parietal owing to character and non-closure of the parieto-squamous suture.

SHRINKAGE AFTER MACERATION

Having subjected them to mummification we next soaked the skulls afresh and macerated them by Leonhart's live steam method. During the process of cleaning after maceration the skulls were kept well soaked and were measured afresh while still dripping wet. The twelve-week drying process was now repeated, the skulls being measured weekly. Table II gives means and

Table II. *Male White crania*, 1922–23.

Number 49. Maceration.

		Mean	S.D.	C. of V.
(F)	Length, S.R.	184·26±·771	8·00 ±·545	4·34± ·296
Macerated	Length, glab.	183·56±·764	7·93 ±·540	4·32± ·294
wet	Breadth	146·12±·539	5·59 ±·381	3·82± ·260
	Aur. Height	117·16±·425	4·41 ±·300	3·76± ·256
(G)	Length, S.R.	182·97±·772	8·01 ±·546	4·38± ·298
Final dry	Length, glab.	182·31±·769	7·98 ±·544	4·38± ·298
dimensions	Breadth	145·04±·546	5·67 ±·386	3·91± ·266
	Aur. Height	116·06±·419	4·35 ±·296	3·75± ·255
(H)	Length, S.R.	1·29±·435	0·452±·308	35·04±2·674
Total	Length, glab.	1·26±·473	0·491±·334	38·97±3·027
shrinkage	Breadth	1·08±·619	0·642±·437	59·44±5·305
	Aur. Height	1·10±·404	0·419±·285	38·09±2·958
(I)	Length, S.R.	1·48		
Complete	Length, glab.	1·53		
shrinkage,	Breadth	1·27		
i.e. B to G.	Aur. Height	1·10		

variabilities for the first and last measurements and the total shrinkage. Comparison with Table I shows that no significant difference occurs in variability whether the crania be measured green, mummified, wet macerated or dry macerated. From this one concludes that both mummification and drying after maceration involve merely dehydration of the bone. It is important also to note that sections (B) and (F) are not sensibly different. I have not thought it worth while to calculate the probability of an essential difference for all dimensions. But a comparison of the supra-orbital length in sections (B) and (F) gives the odds against a real difference between the samples as 33 to 1. Consequently it is apparent that initial mummification, soaking and maceration bring no unforeseen factors into cranial dimensions. Maceration for practical purposes is simply a restoration of the water content and the opposite of mummification or post-maceration drying. No doubt this fact was apparent before, but we have had no evidence to substantiate it until now.

Comparing the means of sections (B) and (F) we see that maceration does not quite restore the original dimensions, but the difference is so slight that it is negligible.

From sections (D) and (H) it is apparent that shrinkage in length is less after maceration than in mummification, whereas shrinkage in breadth and height is greater. The explanation of this difference is not at all clear to me and had better be left for future consideration. The differences in variability

between mummification and maceration are not great except in breadth which apparently shrinks in much more orderly fashion after maceration.

The percentage in shrinkage on the final dry dimensions after maceration is the following:

Supra-orbital length	...	...	0·70 %
Glabellar length ...	...	...	0·69 %
Euryon breadth ...	...	...	0·74 %
Auricular height ...	...	...	0·95 %

These figures relate solely to the shrinkage after maceration. But I have shown that maceration does not quite bring back the dimensions to the original figures. By subtracting the total of the wet macerated dimension in the entire series from the initial green measurement immediately after bisection and taking the mean value we find that after maceration the cranium, on the average, fails to reach its original dimensions by the following amounts:

Supra-orbital length	...	...	0·204 mm.
Glabellar length ...	...	...	0·296 mm.
Euryon breadth ...	...	...	0·163 mm.
Auricular height ...	...	...	0·000 mm.

In auricular height alone is the wet macerated dimension quite as great as the original measurement. If we subtract the values of section (G) from those of section (B) we obtain the total shrinkage from the green state to that of complete drying after maceration. The figures for this complete shrinkage and the percentage of these on final dimensions are:

Supra-orbital length	...	...	1·48 mm.	0·81 %
Glabellar length ...	...	...	1·53 mm.	0·84 %
Euryon breadth ...	...	...	1·27 mm.	0·88 %
Auricular height ...	...	...	1·10 mm.	0·95 %

These are the figures to which we must turn when it is desired to reconstruct the dimensions of the living cranium from those of the dried macerated skull. The shrinkage varies between 0·8 and 1·0 per cent. of the dry dimensions. In my earlier work I estimated the approximate average shrinkage at 1·1 per cent., a figure which was rather large when compared with the result obtained by my colleague Doctor Ingalls on the femur. Undoubtedly that high figure was due partly to the heterogeneous material and partly to the small size of the sample. Probably the figures now given more nearly approach the true average.

COMPARATIVE RATE OF SHRINKAGE IN MUMMIFICATION AND AFTER MACERATION

Tables III and IV give the mean amounts of shrinkage in each dimension for every week in the three-month periods of drying.

In mummification shrinkage tends to increase up to the end of the third week of drying. Thereafter the rate of change is much less, and by eight weeks the cranium has reached the stage when oscillation in dimensions begins

Table III. *Male White cranio*, 1932, 33

Table III. *Male White crania*, 1922–23.

Number 49. Mummification. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Length, S.R.												
Total of 49	19·50	16·25	23·00	7·50	4·00	2·00	0·00	+0·75	1·75	1·75	+4·75	1·00
Av. shrinkage	0·398	0·332	0·469	0·153	0·082	0·041	0·00	+0·015	0·036	0·036	+0·097	0·020
Length, glab.												
Total of 49	22·00	15·50	23·25	6·75	3·00	4·00	1·25	0·00	0·00	+1·50	+2·75	0·00
Av. shrinkage	0·449	0·316	0·474	0·138	0·061	0·082	0·025	0·00	0·00	+0·031	+0·056	0·00
Breadth												
Total of 49	7·20	12·00	13·50	0·50	3·00	2·00	1·00	0·50	1·50	0·00	+1·00	1·50
Av. shrinkage	0·147	0·245	0·276	0·010	0·061	0·041	0·020	0·010	0·031	0·00	+0·020	0·031
Aur. height												
Total of 49	2·50	11·50	13·00	6·50	2·50	3·00	0·25	2·25	2·50	0·25	0·50	+0·75
Av. shrinkage	0·051	0·235	0·265	0·133	0·051	0·061	0·005	0·046	0·051	0·005	0·010	+0·015

The figures given are the total and the average amount of shrinkage in mm. for each week of the drying period. Where a plus sign appears there has been no shrinkage during that week but, on the contrary, an increase in dimension. This fluctuation occurs only when the cranium has shrunk to its approximately final dimensions and is measurably sensitive to variations in atmospheric humidity.

Table IV. *Male White crania*, 1922–23.

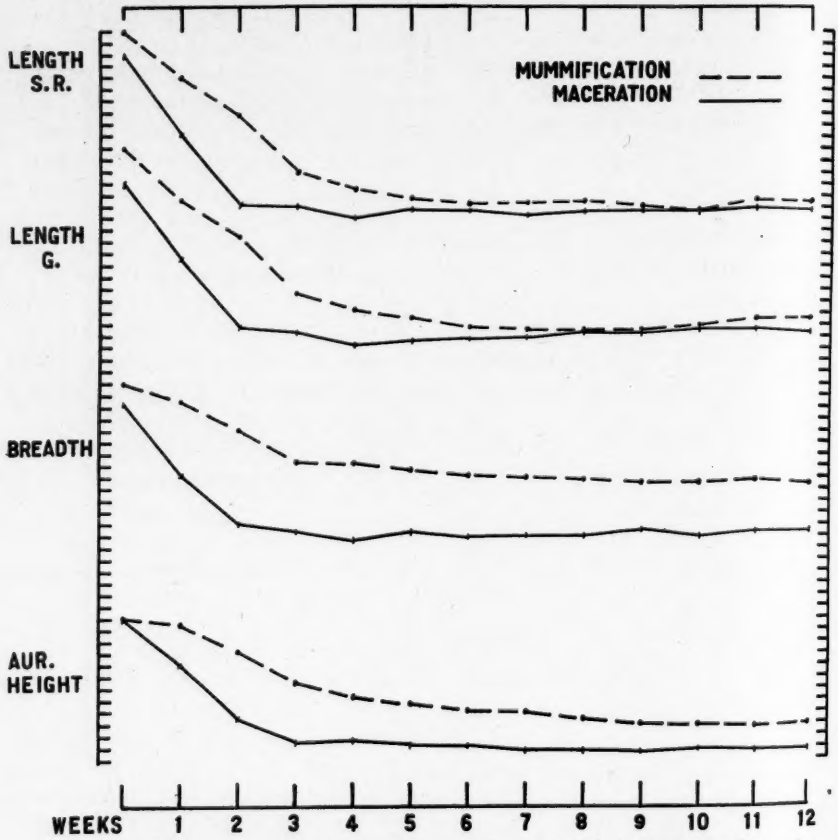
Number 49. Maceration. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	Difference between wet fresh (B) and wet macerated (F)
Length, S.R.													
Total of 49	31·75	29·00	1·00	5·25	+3·50	0·00	1·75	+1·25	+0·50	0·00	+1·25	0·50	10·00
Av. shrinkage	0·680	0·592	0·020	0·107	+0·071	0 00	0·036	+0·025	+0·010	0·00	+0·025	0·010	−0·204
Length, glab.													
Total of 49	31·50	29·00	2·00	4·75	+1·50	+1·50	+0·25	+2·00	0·50	+1·25	+0·50	1·25	14·50
Av. shrinkage	0·643	0·592	0·041	0·097	+0·031	+0·031	+0·005	+0·041	0·010	+0·025	+0·010	0·025	−0·296
Breadth													
Total of 49	30·50	20·00	3·50	3·50	+3·50	1·50	0·00	0·00	+2·00	2·00	+1·50	0·00	8·00
Av. shrinkage	0·622	0·408	0·071	0·071	+0·071	0·031	0·00	0·00	+0·041	0·041	+0·031	0·00	−0·163
Aur. height													
Total of 49	19·25	22·25	10·25	+1·25	1·75	0·25	1·75	0·25	1·00	+1·25	0·00	0·00	0·00
Av. shrinkage	0·393	0·454	0·209	+0·025	0·036	0·005	0·036	0·005	0·020	+0·025	0·00	0·00	0·00

The figures given are the total and the average amount of shrinkage in mm. for each week of the drying period. The plus sign is explained in the legend for Table III. The minus sign in the last column indicates by how much, on the average, the wet macerated cranium fails to reach the measurement of the same dimension in the fresh condition.

to make its presence. This indicates that complete shrinkage has taken place, and thereafter the only change in cranial dimension is produced by sensitivity of bone to atmospheric humidity.

After maceration the greatest shrinkage occurs in the first and second weeks. By that time shrinkage is almost complete, and in the fourth and fifth weeks the oscillations due to atmospheric humidity begin to appear.



Graphic representation of shrinkage of linear dimensions in drying White male crania. Abscissae indicating shrinkage are at 1/10 mm. intervals. Completion of shrinkage is attained in mummification at the end of eight weeks and after maceration at the end of four weeks. Note the oscillation characteristic of cranial dimensions after shrinkage is completed. This is caused by changes in atmospheric humidity.

Practically speaking shrinkage after maceration is complete in four weeks, and in mummification the process only lasts for about eight weeks.

I have attempted to illustrate the facts of shrinkage in the accompanying graph. Shrinkage is completed at the end of the fourth week in maceration,

and at the end of the eighth week, in mummification. The humidity oscillations thereafter are quite apparent. For some unknown reason this sample shows greater shrinkage in length during mummification but in breadth and height after maceration.

SUMMARY

1. A series of 49 male White skulls has been subjected to mummification and later to maceration, measurements being made weekly.

2. Shrinkage in mummification is complete in eight weeks and equals between 0·6 and 0·8 per cent. of the final mummified cranial dimensions.

3. After maceration the cranial dimensions scarcely reach their original value, but, on the average, they come at least to within 0·3 mm. of the green dimensions.

4. After maceration shrinkage is complete in four weeks and the difference in measurement of the dried macerated cranium from the dimensions of the green skull varies from 0·8 to 1·0 per cent. of the final dried cranial measurements.

5. Mummification, maceration and drying after maceration represent, for practical purposes, merely variations in the water content of the bones. No unforeseen factors influence the cranial dimensions as a result of these procedures.

6. In its dry stage the cranium is sensitive to changes in atmospheric humidity, but the alteration in dimension due to this cause is negligible.

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TWO CASES OF MISPLACED FIXED KIDNEYS

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AND
BORIS BOULGAKOW, M.D.
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The two cases which form the subject of this note were found in the post-mortem room of the Medico-legal Department, both being cases of accidental death. They present some interest from an embryological as well as from a practical point of view:

Case No. 1 was found in a man aged 22 years who was normally developed and who was free from abnormalities other than the one to be described.

The kidney is solitary and almost round in shape, measuring 103×101 mm., its surface is lobulated and the pelvis faced the anterior abdominal wall. The upper pole was situated at the level of the fourth lumbar vertebra covering the lowest part of the abdominal aorta and vena cava just above their bifurcation. The lower pole reached the upper part of the body of the second sacral vertebra (Fig. 1). The renal arteries, three in number, arise from the common iliacs and enter the organ from behind (Fig. 2), while the veins and ureters are placed on the anterior surface. The veins are directed upwards and join the vena cava just above the kidney, the ureters pass almost straight downwards to the bladder in front of the rectum and enter the bladder in a normal manner. The left ureter is situated at a lower level than the right, the relative lengths being 186 mm. right and 161 mm. left. They arise just below the veins and are separated from each other by an intermediate lobe of the kidney. The seminal vesicles are unequal in size, the left being 33 mm. long and the right 43 mm. The suprarenal glands are normally developed and are situated in their normal position in the dorso-lumbar region. Microscopically the kidney and suprarenals show no abnormality, but on transverse section of the kidney there were found two lateral pelves with a mass of cortical substance between them more definitely seen in the upper pole.

Case No. 2 was found in a boy aged twelve years who died from a tram accident.

The left kidney was found at the level of the first sacral vertebra, to the left of the middle line below the pelvic brim and beneath the common iliac vessels. The upper pole was directed towards the promontory and its hilum medially and downwards. There are two renal arteries, one arising from the aorta at its bifurcation, the other from the left common iliac; there is one vein

passing to the right common iliac vein. The ureter, short and curved, enters normally into the bladder (Fig. 3). The left suprarenal gland was situated in its normal position in the dorso-lumbar region and was normal in structure. The right kidney was situated in its proper position and was approximately the same size as the left organ.

From the embryological study of the urogenital system it is considered that the origin of the permanent kidney is seen at a very early stage of the embryo as a short canal which begins on the posterior wall of the Wolffian duct close to its opening into the cloaca. This canal is the beginning of the ureter with

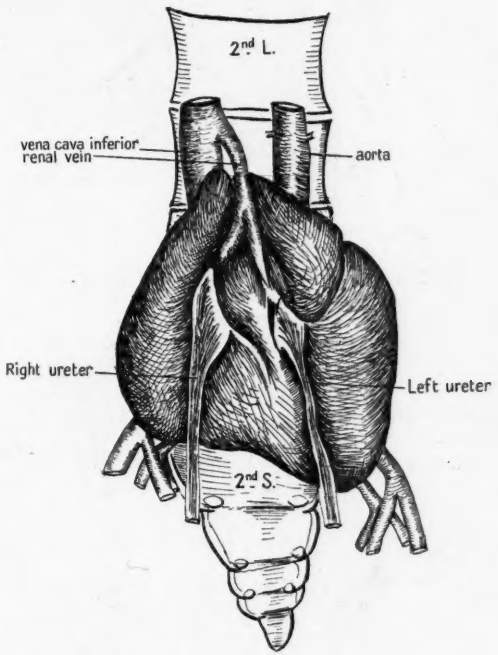

Fig. 1. Anterior surface of solitary kidney.

the pelvis and calyces of the kidney and in development passes upwards to the anterior superior surface of the Wolffian body.

According to Kupfer, about this period the two kidneys are almost spherical in shape, touch each other on their medial surfaces, are situated at the point of bifurcation of the aorta into the two umbilical arteries and fill the space between these two vessels.

According to Young and Thompson the kidney is developed opposite the first sacral vertebra and grows forwards on the dorso-lateral aspect of the Wolffian body. At this stage according to Keith the hilum is directed towards

the pelvic cavity and as the kidney grows towards the suprarenal body it undergoes a rotation so that the hilum is directed inwards and forwards.

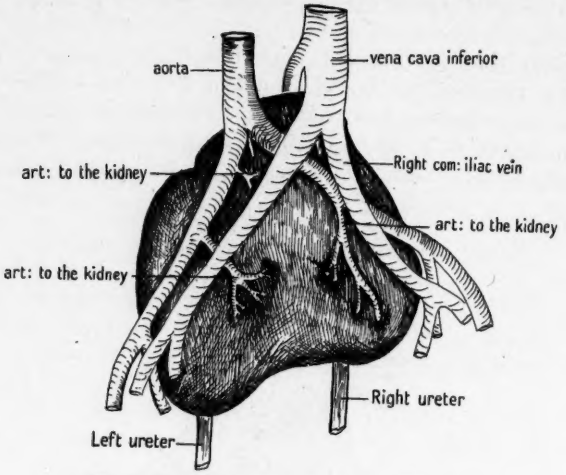

Fig. 2 Posterior surface of solitary kidney.

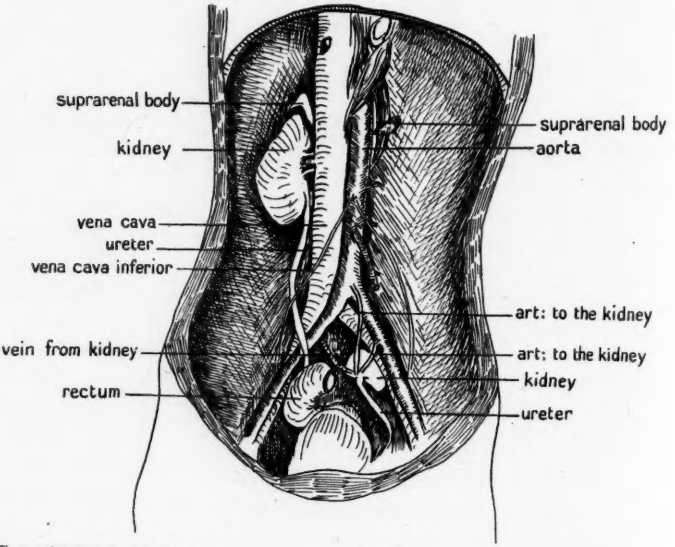

Fig. 3. Case of left misplaced kidney. Note: the left kidney looks smaller than the right one, but it is due to its position under the pelvic brim.

In our first case therefore we may assume that an early fusion of the two organs took place along their medial aspect and fixation occurred in their

normal embryological position. A possible explanation of the fixation may lie in the failure of development of the ureters which might then be assumed to act in the manner of the gubernaculum testis and prevent the kidney following the growth upwards of the body.

In the second case there is no fusion by which fixation could be explained, whereas the left kidney, as in case No. 1, remained in its early embryological position. The normal position of the suprarenals in both cases shows the non-relationship in development of these organs to the kidneys.

From a surgical point of view such displacement of the kidney simulating a tumour is of great importance.

STERNALIS MUSCLE (IN THE LIVING)

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The sternalis muscle, shown in this photograph, was discovered in a male patient in the Royal Hospital, Belfast. The muscle contracted, and then stood well out on the chest, with the recti abdominis in flexion of the trunk, and, as is shown, with the pectorales in adduction of the arms; and its origin could then be seen to spread out transversely over the lower part of the pectoralis major. It showed only feeble movements when the sterno-mastoid muscles were in action and these are probably to be associated with the synergic contraction of the recti abdominis.

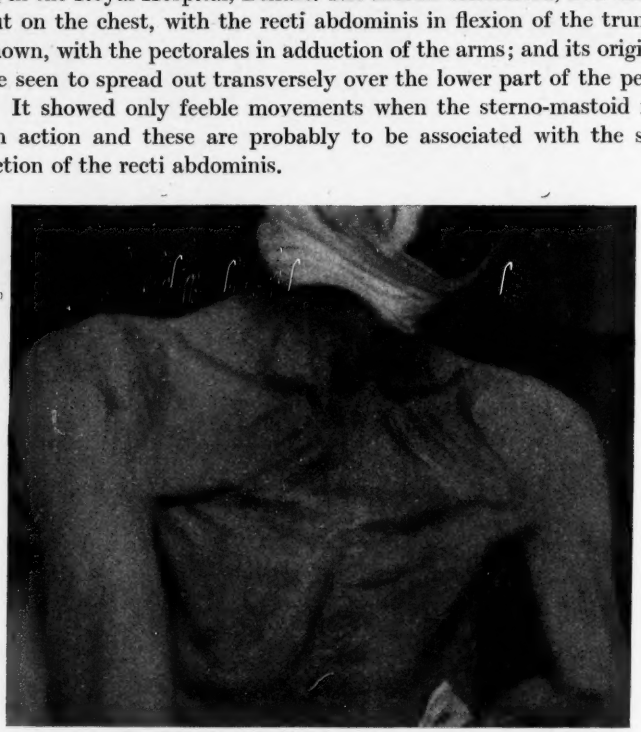

Fig. 1

The sternalis is, of course, a well-known human variation, being found in at least 3 per cent. of adult subjects, and there is now a considerable literature on it, its peculiarities, and its possible homology. Parsons ("On the Morphology of the Musculus Sternalis," *Journ. Anat. and Phys.* vol. XXVII, p. 505) summarises well the known facts about the muscle, while of the more recent papers, as are enumerated in *Quain's Myology*, 1923, that of Yap ("Musculus Sternalis in Filipinos," *Anat. Rec.* vol. XXI, p. 353) contains interesting tables of its occurrences in anencephalous monsters, in the sexes, and in different races. This note adds to the previous records the "actions" of the muscle.

THE MIDDLE SACRAL ARTERY IN THE HORSE

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The following anomalous condition of the arteries of the tail of the horse may be of interest. The subject was a dissecting room pony, and showed no other abnormalities of the circulatory system.

The first point noticed was the presence of a distinct middle sacral artery arising at the angle of bifurcation of the two hypogastric arteries, and main-

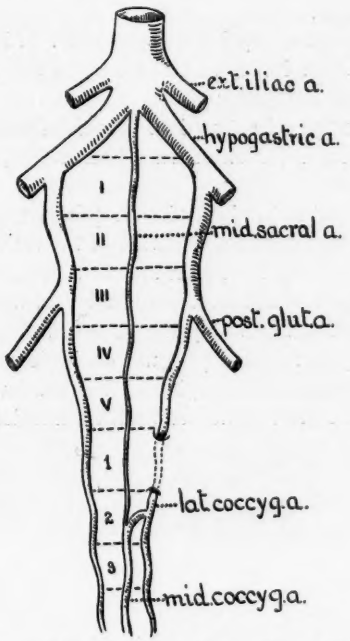

Fig. The Roman numerals refer to the relative positions of the Sacral Vertebrae, the Arabic numerals to the Caudal Vertebrae.

taining the continuity of the aorta as is normally the case in the ox. This middle sacral artery was continuous with the middle coccygeal artery, which occupied a median position on the ventral aspect of the caudal vertebrae. As the course of the middle coccygeal artery was followed, it was found to undergo a sudden increase in calibre, due to its being reinforced by a con-

siderable branch of the left lateral coccygeal; the latter vessel being the caudal continuation of the lateral sacral artery.

The course of the left lateral coccygeal artery was also unusual. The left lateral sacral artery pursued its normal course on the ventral aspect of the sacrum. Between the last sacral vertebra and the first caudal it disappeared from the ventral aspect of the vertebral column and was continuous with a vessel disposed on the dorsal aspect of the transverse process of the first caudal vertebra. The artery reappeared between the first and second caudal vertebrae, gained the ventral aspect of the coccyx, and was normal in position for the rest of its course. Opposite the second caudal vertebra it gave off its large supplementary branch to the middle coccygeal artery (vide fig.).

On the right side, the lateral sacral artery and its continuation the lateral coccygeal artery were normal.

The normal arrangement of the arteries in the sacral and caudal regions of the horse is as follows:

(*a*) The middle sacral artery is usually absent. If it is present it is quite a small vessel, which terminates in the fascia on the ventral aspect of the sacrum.

(*b*) The middle coccygeal artery is a branch of one of the lateral sacral arteries and is not a continuation of the middle sacral, even when the latter vessel is present.

The case is of interest not only for its comparative rarity, but also for the fact that it must be regarded as a retention of the caudal aorta in the horse, a condition which is normal in the ox and to a certain extent in man. The explanation of the position of the commencement of the left lateral coccygeal artery is not very obvious. Possibly the normal vessel was present at some early stage, was subject to some pressure during development and growth whereby it was obliterated in the region of the first caudal vertebra, and the continuity of the vessel was maintained by the dilatation of a retro-transverse anastomosis.

VARIATIONS OF THE OCCIPITO-ATLANTAL JOINT IN RELATION TO THE METAMERIC STRUCTURE OF THE CRANIO-VERTEBRAL REGION

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INTRODUCTION

The morphology of the cranio-vertebral region and the explanation of congenital variations of the atlas and occipital bone are subjects which have engaged the attention of comparative anatomists and evolutionary biologists for many years. More recently a considerable advance has been made in the study of these complex problems by embryologists such as v. Ebner, Froriep and Barge. We shall give an account of this work and discuss the current views on the subject after having described certain specimens which illustrate the principal types of variation in this region. We think it necessary, however, to allude in the first place to certain anatomical and embryological facts which form the basis of the discussion, and secondly we propose to discuss a factor in the etiology of congenital variations in general which introduces a new element into the problems of inheritance and variation. This factor leads us to a consideration of these subjects from a somewhat different aspect to that which has hitherto been the commonly accepted standpoint and one which appears to us to be of great importance as well as a fundamental element to be considered in the explanation of certain features which are commonly present in these types of congenital variation.

This standpoint is a tendency towards instability in the normal development of the individual which may be induced by a weakening of the vitality of the germ-cells or by changed conditions influencing ontogeny, examples of which we shall allude to later.

DESCRIPTION OF SPECIMENS

The *first* specimens which we shall describe, illustrate the changes from the normal which accompany the incorporation of a cervical vertebra with the skull.

Specimen 1 is an example of fusion of the atlas with the occipital bone and of the axis with the third cervical vertebra. This specimen is from the Museum of King's College Hospital, and figs. 1, 2 and 3 represent the main features of the specimen as seen from the front, back and side. The atlas is incompletely fused with the occipital bone and is placed very obliquely; the

transverse process of the right side being 1 cm. below the level of that on the left. The lateral masses are united by bone with the condylar portion of the occipital, there is a gap however between the anterior arch and the under surface of the basilar process. The posterior arch is joined to the edge of the

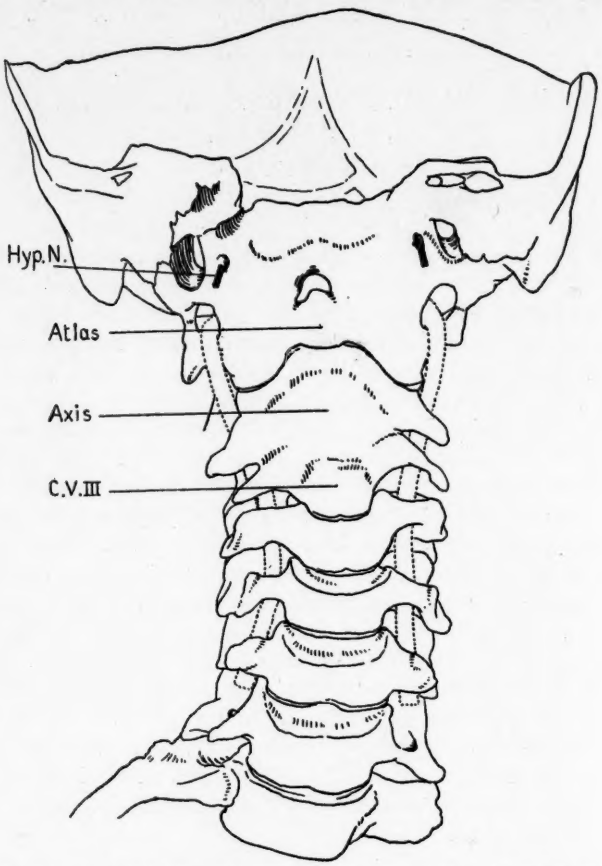

Fig. 1 (Specimen 1). Fusion of atlas with occipital bone, and of the axis with the third cervical vertebra. The specimen is seen from the front. The course of the vertebral artery has been represented on each side by dotted lines, and that of the hypoglossal nerves by bristles passed through the anterior condylar foramina.

foramen magnum laterally, but a gap, 1 cm. in length, is present medially and behind, and also on each side at the base of the arch where there is a foramen for the vertebral artery and suboccipital nerve; the arch shows a median suture in the position of the tubercle indicating incomplete fusion of its right and left halves. A foramen is present (see fig. 2) at the junction of the base of the neural arch with the transverse process, which in all probability trans-

mitted a vein. The anterior arch presents the usual facet for articulation with the odontoid process of the axis. The odontoid process does not articulate directly with the occipital bone at the anterior margin of the foramen magnum, but in this situation there is a notch bordered on each side by two

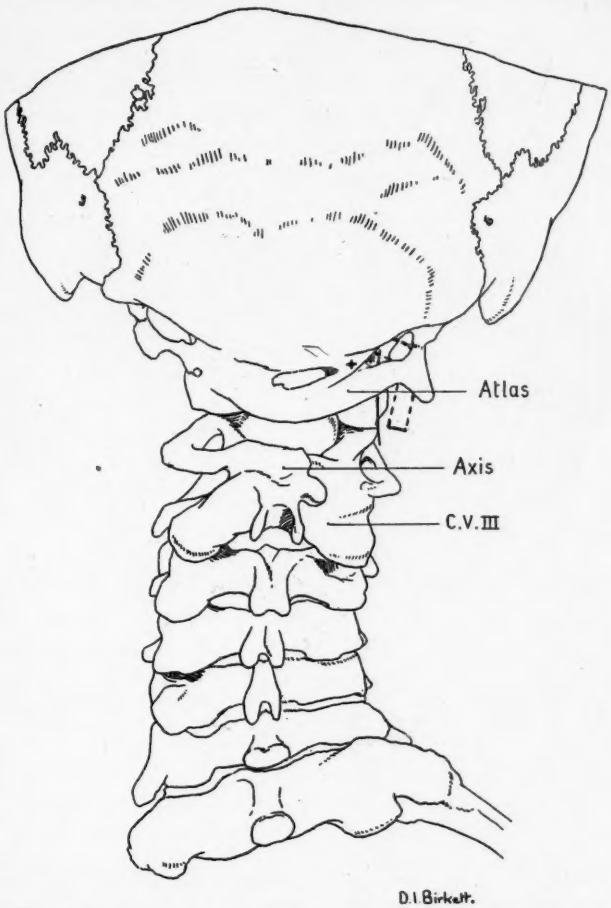

Fig. 2. The same specimen viewed from behind. Note the irregular fusion of the spine of the axis with that of the third cervical vertebra, and the large size and bifid character of the latter. A bristle indicates the position of the venous foramen at the root of the posterior arch.

lateral spines. The anterior condylar foramen is well seen in fig. 1. The transverse process lacks the costal element and is united to the jugular process of the occipital bone by a bar of bone passing obliquely backwards. On the right side a bridge of bone forms a foramen with the former process and appears to have transmitted a vein. A large posterior condylar foramen is

present on each side. The course of the vertebral artery is indicated in fig. 1, where it lies in front of the true transverse process of the atlas and turns backwards round the fused superior articular process of the atlas and occipital condyle. The farther course of this vessel is indicated in fig. 2, where it is

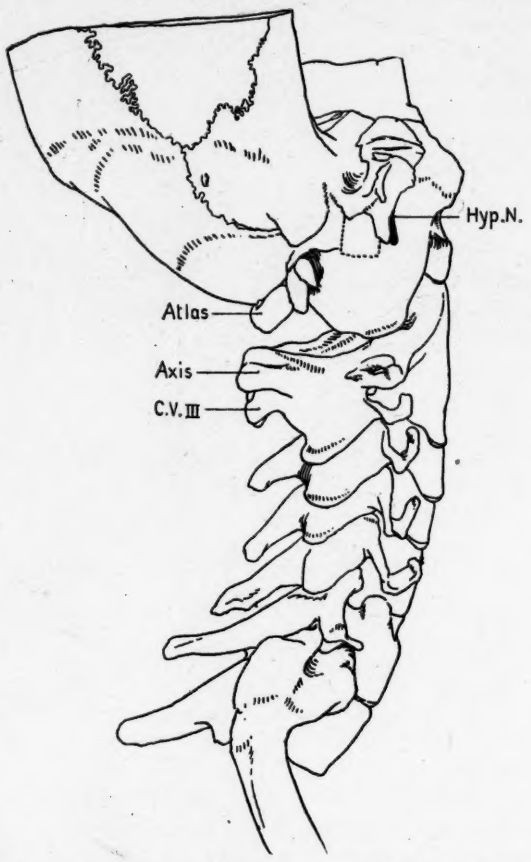

Fig. 3. The right aspect of the same specimen showing the foramen between the occipital bone and atlas, for the vertebral artery and the suboccipital nerve; also the fusion of the transverse process of the atlas with the jugular process of the occipital bone. Note also the direction of the posterior arch of the atlas, which appears to be bent downwards by the pressure of the occipital bone.

seen passing through the foramen at the base of the neural arch in its passage towards the foramen magnum. The inferior articular facets are more rounded than usual and approach the form assumed by the occipital condyles. The inferior articular processes are prolonged downwards farther than is normally the case, especially on the right side, and the facet for the axis is prolonged

upwards on its medial aspect to articulate with the base of the odontoid process.

The axis is fused below with the third cervical vertebra. A groove on the anterior surface indicates the junction of the bodies of these two vertebrae. The neural arches are completely fused with the exception of the gap at the intervertebral foramen. The spine of the axis lies considerably to the right of the spine of the third cervical vertebra. The spine of the third cervical vertebra is large and markedly bifid, and it thus resembles that of the second.

The odontoid process is remarkable for the extent to which the superior articular facet of the axis is carried upwards on to its lateral aspect. It presents the usual facets for the anterior arch of the atlas and transverse

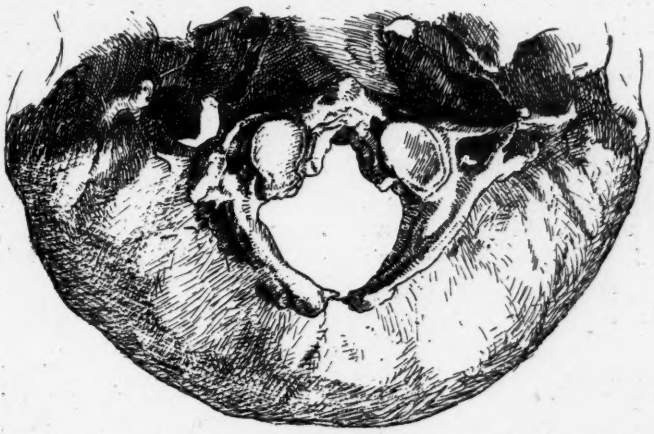

Fig. 4 (Specimen 2). Fusion of the atlas vertebra with the occipital bone. Note the foramen in the transverse process for the vertebral artery; the approximately circular outline of the inferior articular facets, and the facets for the odontoid process of the axis. Note also the asymmetrical position of the bone; on the left side the transverse process of the atlas is fused with the styloid process, on the right side it is separated from the styloid process by a distance of 2 cm.

ligament. Apart from the fusion of the third cervical vertebra with the axis and its large bifid spine, this vertebra does not depart markedly from the typical. The costal element of the transverse process is however slender and placed very obliquely.

The sixth cervical vertebra shows the usual prominent carotid tubercle, and on the right side the foramen is subdivided into two by a bar of bone which will have separated the vertebral artery from a vein. A separate foramen, presumably for a vein, is also present in the transverse process of the 5th cervical vertebra. The 7th cervical vertebra has transverse processes having the usual characters for this vertebra, namely, a large true transverse process, a small costal element and a small foramen. The spine is prominent but considerably less so than that of the first dorsal vertebra.

Specimen 2 (fig. 4) is another example of fusion of the atlas with the occipital bone. The form of the atlas is complete with the exception of the posterior neural arch, the two halves of which have failed to unite behind. The anterior arch is completely fused with the under surface of the basilar process of the occipital bone. There is, however, a deep groove separating these parts in front. Behind the arch there is an irregular mass of bone which must have surrounded the odontoid process of the axis. There is no distinct facet on the posterior surface of the anterior arch of the atlas for the odontoid process, but there are two lateral facets which are probably adventitious. A well-marked anterior tubercle for the attachment of ligaments and the longus colli muscles is present. The posterior arch of the left side is free, whereas that on the right side is fused with the margin of the foramen magnum except at its base where there is a curved canal for the passage of the vertebral artery. In addition to this foramen there is a posterior condylar foramen in the occipital bone leading to the terminal part of the lateral sinus and above both these also in the occipital bone is a hypoglossal or anterior condylar foramen. A gap of 3 mm. width is present between the extremities of the two halves of the neural arch.

The transverse processes are markedly asymmetrical, each is traversed by a foramen for the vertebral artery. The left process is the more prominent and consists of a slender costal element which is joined by a spicule of bone to the base of the styloid process. The true transverse process is of large size and is in contact with but not joined to the jugular process of the occipital bone. The right transverse process is bent downwards so that the costal element slopes downwards at an angle of 45° with the horizontal. It lies immediately internal to and below the inner margin of the jugular foramen. The distance between the transverse process and the styloid process on this side is 15 mm., whereas on the left side it is joined to it; there is thus a considerable amount of rotation between the occipital bone and the atlas. The inferior articular facets on the under surface of the lateral masses are slightly concave; that on the left side has the usual approximately circular outline, that on the right side is prolonged for a short distance backward into the base of the posterior arch. In addition to the rotation of the bone there is a considerable difference in the level of its transverse processes, the left being lower than the right, although this difference is masked by the bending downward of the transverse process on the right side.

On looking at the base of the skull from the inside, it is seen that the condylar region of the occipital bone and its basilar process are bulged up into the posterior cranial fossa as if pressure had been exerted in a downward direction on the head, which had been resisted by counter-pressure of the vertebral column. The width of the foramen magnum in front is encroached upon by the formation of the irregular masses of bone previously referred to, which have been formed round the odontoid process of the axis. These appearances suggest that the fusion of the atlas with the occipital bone may

have been caused by prenatal disease which had prevented the normal formation of the occipito-atlantal joints and produced other deformities and defects in development.

There is an obvious elongation of the transverse diameter of the posterior cranial fossa with a corresponding diminution of its antero-posterior diameter, which gives one the impression that the deformity has been caused by pressure on the skull from above.

Our remaining three specimens illustrate the condition which is usually described as manifestation of an occipital vertebra. Specimen 3 (fig. 5) shows the basal portions of the posterior arch of such a vertebra and it will be seen that these project backwards a distance of about 1/3 inch from the condylar

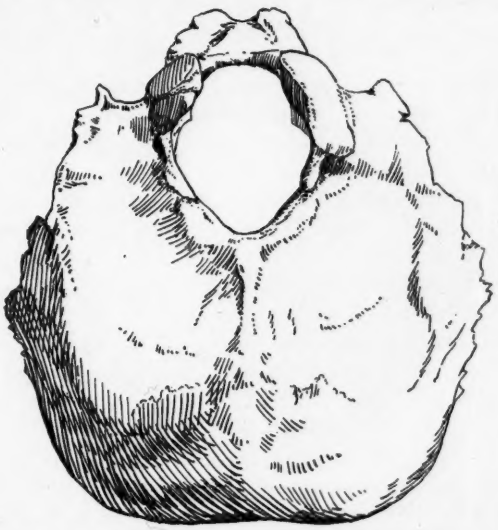

Fig. 5 (Specimen 3). Manifestation of the basal portions of the neural arch of an occipital vertebra. The inferior articular facets have the form of occipital condyles. There is no foramen for the vertebral artery, and no facet on the anterior arch for the odontoid process of the axis.

portion on the under surface of the margin of the foramen magnum. The posterior condylar fossae are deep and a posterior condylar foramen is present on each side. The condylar facets have the usual characters of the occipital condyles, namely they are oval, with the long axis directed obliquely forward and inward; the articular surfaces, directed downward, and laterally, are markedly convex from behind forwards. On the right side the main condylar surface is sub-divided into an anterior and a posterior articular facet by a non-articular groove. The anterior margin of the foramen magnum presents a normal appearance. The anterior condylar foramen on the left side is partially divided by a spicule of bone, on the right side it shows no sign of sub-division.

The next specimen (fig. 6) shows a further degree of separation of an occipital vertebra. The two halves of the posterior arch extend backward around the posterior half of the foramen magnum to within a quarter of an inch of the opisthion. The anterior or hypochordal arch is represented by two processes which project forward and inward toward the median plane and end in rounded tubercles, separated from one another by an interval of a sixth of an inch. As in the previous specimen the posterior condylar fossae are deep and a posterior condylar foramen is present on each side. The articular surfaces for the atlas have the typical appearance of the occipital

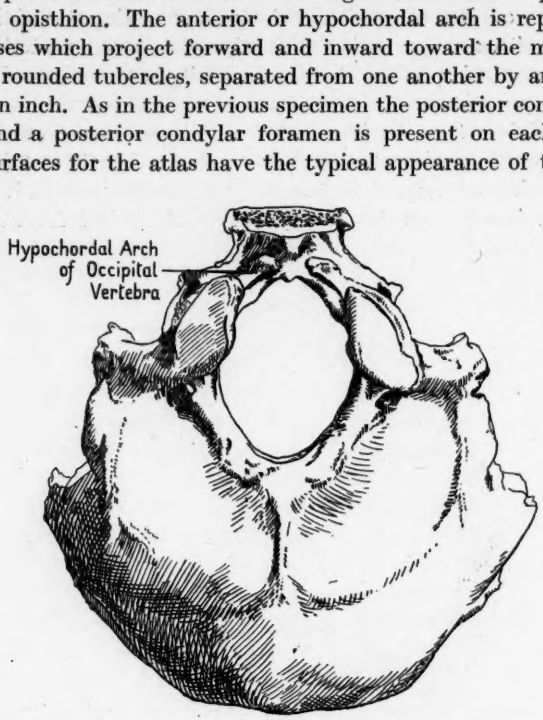

Fig. 6 (Specimen 4). Manifestation of the basal portions of the hypochordal arch of an occipital vertebra, with a slight indication of the two halves of the neural arch which is outlined in relief round the posterior margin of the foramen magnum.

condyles. The jugular processes are well defined and there is no indication of an arterial foramen. The anterior condylar foramina are unusually large.

Our last specimen, fig. 7, was obtained from a student's disarticulated skeleton of which the vertebral column did not appear to correspond to the skull. It represents a more advanced stage in the formation of the hypochordal arch of an occipital vertebra than the preceding specimen, fig. 6. In this specimen the hypochordal arch is complete. It is fused throughout its whole extent with the anterior margin of the foramen magnum. It does not bear a facet for the odontoid process of the axis and thus differs from the normal anterior arch of an atlas. It bears two small tubercles on its under surface which are situated in the median plane, one in front of the other, and which probably serve for the attachment of the longus colli muscles, and ligaments. The articular surfaces for the atlas have the ordinary appearance

of occipital condyles as in the preceding specimen. Indications of a posterior arch are not pronounced, on the left side there is a large posterior condylar foramen and deep fossa, on the right side the foramen is absent. The anterior condylar foramen on the right side is sub-divided, on the left side it is complete. The transverse processes are unusually prominent but are not separated from the occipital bone except on the right side, where there is a slight notch seen on the posterior aspect. On looking at the base of the skull from the inside, the occipito-sphenoid plate formed by the basilar process and dorsum sellae is seen to be unusually long.

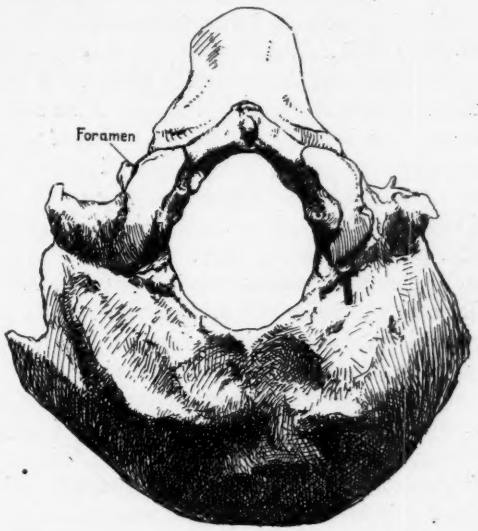

Fig. 7 (Specimen 5). Hypochordal arch of an occipital vertebra. The inferior articular facets have the usual form of the occipital condyles. There is no facet on the anterior arch for the odontoid process of the axis. The transverse processes have no foramen for the vertebral artery, nor is a foramen for the artery present between the posterior arch and occipital bone.

MORPHOLOGY OF THE CRANIO-VERTEBRAL REGION

The older "vertebral theory" of the skull, which was put forward by Goethe and Oken, and in our own country was supported by Owen, has in recent times been modified, and the question of a vertebral origin of the cranium is now limited to the post-otic segment of the skull; for although three pro-otic somites, and head cavities anterior to these, are present, these segments have not given rise to typical vertebrae. The anterior portion of the skull is regarded as the older part and is termed by Fuchs "Palaeo-neurocranium" or shortly Palaeocranium. This part has apparently been evolved as a primary protective covering for the brain and sense-organs at a period before the development of a spinal column and is therefore not evolved by the modifi-

cation of previously formed vertebrae, whereas, that part of the skull which lies behind the otic vesicles shows in the embryos of higher types of vertebrate animals a segmented structure which is similar to that of the true spinal column. This part has been termed the "Neo-neuro-cranium" or shortly Neocranium. It includes the occipital part of the skull and is usually regarded as an addition to the Palaeocranium by transformation of the anterior part of the vertebral column. This transformation involves the skeletal elements and there is also an inclusion of certain of the anterior spinal vessels and nerves in the cranium.

In the cyclostomes the unsegmented Palaeo-neuro-cranium is the only part of the skull which is present, and there is neither a true vertebral column nor any evidence of the skull having been formed from vertebrae. The neural plates or "arcualia" however, two of which correspond to each complete spinal nerve, extend forward on the dorsal aspect of the notochord as far as the skull, and are the first indication of the formation of neural arches.

In the lamprey (*Petromyzon marinus*), the dorsal and ventral roots of the spinal nerves are separated by the neural plates or cartilages. The ventral root of each spinal nerve lies behind the anterior neural cartilage, and the dorsal root behind the posterior cartilage. The nerves and cartilages thus alternate with each other in an antero-posterior direction. The anterior neural cartilages are believed by Schauinsland to correspond to the interneural, interdorsal or intercalary plates of higher types of fishes, and the posterior neural cartilages to the neural arches or basi-dorsal plates.

The significance of the alternating arrangement of the myotomes with their motor nerves and the intersomitic septa with their segmental arteries and dorsal or sensory nerves has been discussed by Primrose in an article, published in this *Journal*, vol. LV (see fig. 13). In dealing with the origin of segmented types of animals from an older non-segmented type, he clearly shows the compound nature of the sclerotomes which is unmistakeably revealed in the more primitive types of vertebrate animals such as the Cyclostomes and Selachia.

Between the otic capsules in the lamprey a cartilaginous "occipital" arch bridges across the medulla oblongata in front of the origins of the glosso-pharyngeal and vagus nerves; which nerves pass out freely behind the skull, instead of through apertures in its wall.

The ventral roots of the more posterior of those spinal nerves which arise in the region of the "branchial basket" join to form the "hypoglossal" nerve. This turns round the posterior end of the basket, and then courses forward beneath it to supply the hypoglossal musculature.

In the Selachia there is usually a definite occipital joint, marking off skull from vertebral column. This is however not present in Hexanchus in which there is a long occipito-spinal region, and the skull is not clearly marked off from the vertebral column.

In *Scyllium Canicula* and in *Heterodontus Philippi*, the Port Jackson

shark, which is the only living representative of this ancient sub-order, which is said to date back beyond the Carboniferous epoch (G. R. de Beer), the presence of the three slender occipital nerves which arise from the lower part of the medulla oblongata below the roots of the vagus, and pass through foramina in the occipital region of the skull, and which in Scyllium form a common trunk with the first five spinal nerves, may be regarded not only as evidence of this part of the skull being segmental in origin, but also that it is developed in serial continuity with the vertebral column. The number of the occipital nerves piercing the skull however varies in different groups, e.g. in Hexanchus there are five occipital nerves, and the position of the occipital articulation relative to the spinal nerves is therefore also variable. It may farther be assumed that the occipital region of the Selachia corresponds to the post-auditory region of the lamprey, the segmental nature of which we have already seen is indicated by the presence of the neural plates, and the relation of these to the spinal nerves.

In the amphibia, e.g. *Rana temporaria*, what is commonly known as the first cervical nerve leaves the vertebral column between the first and second vertebrae. It is distributed to the tongue and adjacent muscles of the floor of the mouth and is generally believed to represent the hypoglossal nerve of mammalia. The total number of vertebrae in front of the urostyle in the frog is nine, of which only one is regarded as cervical. This ring-like first vertebra of the spinal column of the frog is probably not homologous with the atlas vertebra of the mammalia. According to Wiedersheim, it represents a vertebra more posterior in the series. The position of the first cervical vertebra of the frog, anterior to the nerve which supplies the muscles of the tongue, suggests that the more anterior spinal nerves which supply the tongue in the cyclostomes, and those which form the occipital nerves of the Selachia, have disappeared in amphibia, and that the tongue in the amphibia is supplied by spinal nerves which are more posterior in the series.

As is well known, the vertebral elements which are present in the elongated tail of the tadpole undergo retrogressive changes and become fused into a single bone, the urostyle, whereas, in the tailed amphibians these elements undergo ossification and persist throughout the life of the animal. It is obvious therefore that extensive retrogressive changes have taken place at both ends of the vertebral column in the Ecaudata, and that in tracing the phylogenetic history of the skull and vertebral column of the higher mammalia we must commence at a stage represented by a lower type in the vertebrate series than the amphibia.

In reptiles, there is in the Ophidia an enormous lengthening of the vertebral column, which in some snakes is composed of more than 300 vertebrae. In the evolution of such a vertebral column, it is probable that lengthening has taken place by addition at the cranial and caudal ends, although it is possible that lengthening may have taken place by sub-division of central somites so that new vertebrae with their accompanying ribs, segmental muscles, vessels

and nerves are interpolated into the series. Some of the most interesting facts bearing upon the comparative anatomy of the occipito-atlantal region are to be met with in other orders of the class reptilia, e.g. in the Crocodilia, Chelonia and Hatteria, among which may be mentioned the so-called "proatlas," found in the crocodiles, and alligators; we do not however propose to deal with this aspect of the question here, as it has quite recently been approached from the embryological standpoint by various authors and more especially by Barge (3) in his monograph "Probleme in kranio-vertebralgebiet." This author believes that the "proatlas" of the alligator represents the cranio-vertebral semi-segment of the neural arch of the atlas, which has not united with the caudal part as it does in the compound neural arch of the mammalia; and that as it does not represent an additional vertebra developed in front of the atlas, the term "proatlas," if used in the sense in which it was originally employed, is misleading and incorrect.

In Sphenodon, Wyeth (30) has shown that an ontogenetic reduction of the number of roots entering into the composition of the hypoglossal nerve takes place, and also of the number of foramina for their exit in the pleuro-occipital cartilage. Thus the rootlets, five in number in "stage *P*," are in "stages *R* and *S*" reduced to four, "these leave the cranial cavity in an antero-posteriorly arranged series of three small foramina the most anterior of which perforates the pleuro-occipital cartilage immediately ventral to the posterior boundary of the foramen jugulare. In the adult condition only two foramina persist (Howes and Swinnerton, 1901). These roots unite to form one main nerve trunk which passes between nerves X and XI."

In the mammalia, as is well known, there is evidence, in certain orders, of diminution in length by fusion of vertebrae which has taken place in the region which we are specially considering, namely the cervical; e.g. in the cervical region of the Cetacea. Moreover in the mammalia, as in lower vertebrates, suppression of muscle and nerve segments has taken place in the occipital region. This is evident on considering the ontogeny of the occipital segments. In the early embryonic stages there appear to be at least three occipital myomeres, these afterwards disappear; and there are three principal groups of ventral roots of the hypoglossal nerve. In ungulates there are also three dorsal roots with their spinal ganglia, which may persist in the calf up to the time of birth (Wilson). In the human subject the 3rd or last of these dorsal roots with its accompanying ganglion, first described by Froriep, is present in the embryo but it afterwards disappears, and the three ventral roots become joined into the single motor nerve of the tongue.

In the amphibia it is probable that suppression has taken place to a greater extent than in the mammalia, the more anterior occipital nerves having disappeared, and the tongue having derived its nerve supply from spinal nerves which are farther back in the series. In the mammalia there is also evidence of suppression of segments and shortening at the caudal end, similar to that which takes place in the ontogenetic development of the frog's

tail. This occurs in the normal development of the coccygeal region in the human subject, in whom, in the 10 mm. stage of the embryo, there are from 10–12 coccygeal sclerotomes, the more distal of which afterward disappear.

In the occipito-atlantal region a modification has taken place in the typical form of the vertebral segments in order to provide a moveable joint at the junction of the head with the spinal column, and it is in this situation that the changes with which we have to deal take place.

In the course of evolution this cranio-vertebral articulation appears to have shifted backward, one vertebra after another having been absorbed into the skull to form its post-otic segment. The position in which the cranio-vertebral articulation has been evolved was possibly determined in the ancestral forms of lower types of living fishes by the relation of the skull to the branchial apparatus and pectoral girdle and would have varied in position according to the greater or lesser development of the branchial region.

In considering this question it is important to bear in mind that a vertebra, such as the first cervical in the frog, does not necessarily correspond to the atlas vertebra of the mammalia, and that in tracing the evolution of the mammalian stock from an early vertebrate type in which the spinal column has not been completely laid down, one must bear in mind that the descent of the mammalia is probably from a different branch of the phylum from that which has given rise to the living types of amphibia. And, although the first spinal nerve in the frog is distributed to the tongue, this does not necessarily imply that the hypoglossal nerve of the mammalia corresponds to the first spinal nerve in the amphibia. It seems probable that in certain classes of vertebrate animals additions to the spinal column and the corresponding muscle-segments, vessels and nerves, have taken place at the cephalic end of the column behind the cranio-vertebral articulation and that the more anterior sclerotomes have fused together to form the post-otic segment of the cranium. Moreover the accompanying myotomes, spinal nerves, and vessels, are in like manner modified, and their original segmental arrangement becomes masked by fusion as is the case with the hypoglossal nerve, or suppression as is seen in the vessels and muscle segments.

It has sometimes been assumed that additions to the vertebral column have taken place by a sub-division of sclerotomes in the centre of the series which have already been laid down, and that in this way vertebrae have, so to speak, been intercalated between elements which are already formed. We are inclined to admit the possibility of such a mode of development, but consider that the evidence on which it is based may be interpreted in another way. Occasionally as in a specimen described by one of us (C. P. G. W.) half-vertebrae are present in the spinal column. These vertebrae when they occur in the thoracic region are frequently accompanied by absence of the corresponding rib, intercostal muscles, vessels and nerves. Thus in the specimen cited, on the side corresponding to the half-vertebra, there were twelve ribs, while on the opposite side eleven ribs only were present and it seems probable

that the abnormality may be explained by assuming the suppression or want of development of a half-vertebra, rather than the intercalation of an additional vertebra into the spinal column. In cases of apparent addition to the vertebral column, for instance those in which thirteen pairs of ribs are present, it is usually found that compensation has taken place in one region of the spinal column by modification of the vertebrae in another so that the lumbar region in the instance quoted is maintained at the normal number (5), in the human subject by modification of the first sacral vertebra, so that it assumes the characters of a fifth lumbar and it is therefore unnecessary to

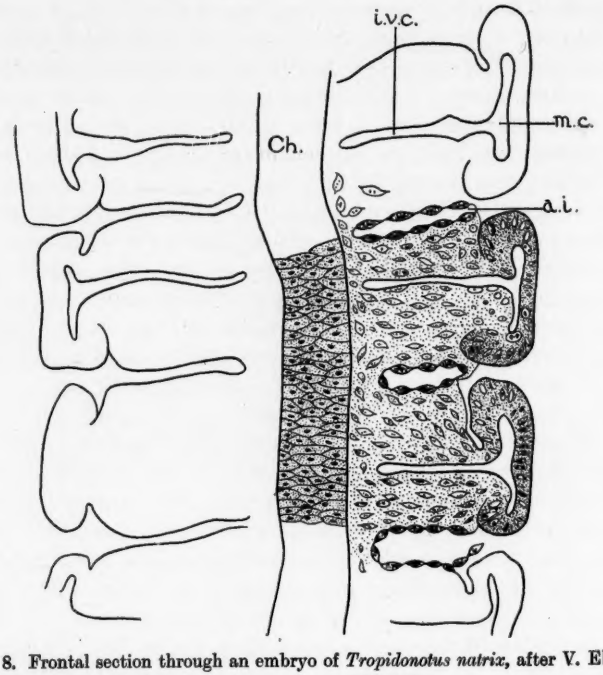

Fig. 8. Frontal section through an embryo of *Tropidonotus natrix*, after V. Ebner.

Ch. Chorda dorsalis. *mc.* Myocoel.
ivc. Intervertebral cleft *a.i.* Arteria interprotovertebralis.

regard the condition as due to intercalation. Similarly, the question of loss of a vertebra in the middle of the series by disappearance of a vertebra, which has already been evolved, although it may occur in an individual as a defect of development, appears to us as an unlikely process in phylogeny. This has been assumed to be the case however, in connection with the so-called "proatlas" of the reptilia which was believed by Albrecht to have been the remnant of a vertebra situated between the atlas and the occipital bone, and which in the course of evolution has completely disappeared in the higher types of the vertebrata. This question has been exhaustively discussed by

the Dutch anatomist Barge, who has studied the development of the cranio-vertebral region of the sheep; he has shown that the cranio-vertebral boundary or articulation between the occipital condyles and the atlas is situated between the caudal segment of the last hypoglossal sclerotome and the cranial segment of the first spinal sclerotome, fig. 10, and that the atlas thus consists of three elements, namely, the cranial and caudal segments of the first spinal sclerotome, and the cranial half of the second spinal sclerotome. It may be as well to recall here the work which was originally carried out by v. Ebner in *Tropidonotus natrix*, or ringed snake, in which he demonstrated that the inter-vertebral disc between the bodies of two adult vertebrae corresponds in position to the intrasomitic cleft which is formed as an extension inwards of the myocoel towards the notochord, and that the intersomitic cleft, marked by the presence in the embryo of the "arteria interprotovertebralis," corresponds in position to the centre of the body of an adult vertebra, fig. 8. The body of each vertebra was thus shown to consist of two semisclerotomes, namely the caudal half of the sclerotome in front joined with the cranial half of the sclerotome next behind.

It will be noted from the diagram, fig. 10, that the spinal nerve is always situated in the light, slightly stained, cranial half of the sclerotome and that in the case of the atlas vertebra, two nerves are included, namely, the first and second spinal. This interpretation of the relationship of the atlas to the embryonic sclerotomes accounts for the serial position of the first spinal nerve in its relationship to the vertebral column and skull, without having to believe that a vertebra corresponding to the first cervical nerve has disappeared. Thus the axiom formulated by Albrecht that *for each spinal nerve there is a corresponding vertebra*, is confirmed without assuming that a vertebra has fallen out of the series. It will be remembered that the suboccipital nerve and vertebral artery in the human subject frequently pass beneath the bony arch extending from the superior articular process of the atlas to its transverse process and known as the ponticulus lateralis. A similar bridge is also found connecting the superior articular process with the base of the neural arch beneath which the vertebral artery and suboccipital nerve pass; this bridge is known as the ponticulus posterius. In fig. 2 (specimen 1) such a bridge is seen passing above the foramen for the vertebral artery and suboccipital nerve, from the region of the superior articular process of the atlas to the neural arch, and may be regarded as evidence in favour of Barge's theory of the composite nature of the atlas. This bridge is indicated in the diagram by an "X." In most mammals the canal for the artery and nerve is normally present, and the relationship of the suboccipital nerve to the atlas in these animals is regarded by Barge as additional evidence of the compound nature of the bone. Barge moreover regards the occasional presence of a foramen or foramina (Foramen arcuale medianum) in the posterior arch of the atlas as an indication of its composite structure. In some cases, where two of these foramina are present, they lie at the bottom of a deep groove separating an upper or cranial from a lower or caudal part of the arch.

It will thus be apparent that the significance of the words "pro-atlas" and "intercalated vertebra" as these terms have been employed in the past, has gradually changed, and in using these terms care must be taken to distinguish between a fully developed and typical vertebra and the scleromeres from which these are developed. Scleromeres (see fig. 12), are developed on the cranial side of those scleromeres which will give rise to the atlas and succeeding vertebrae. These scleromeres are spoken of as the hypoglossal or occipital, and in relationship with them are the segmental nerves

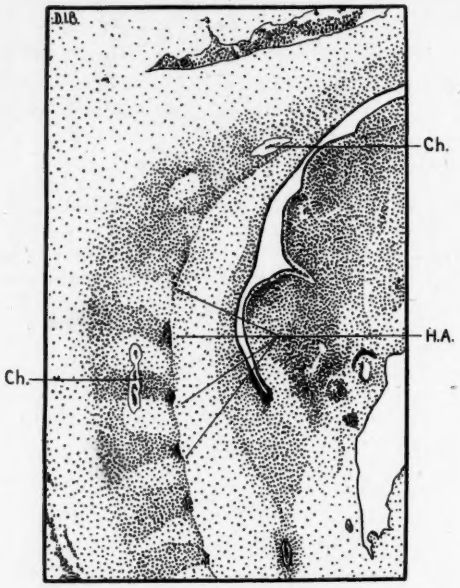

Fig. 9. Sagittal section through the occipito-atlantal region of a 12 mm. human embryo showing the dark and clear areas of the sclerotomes. Ventral to the dark areas are seen the rudiments of the more deeply stained hypochordal arches (*H.A.*). The notochord (*Ch.*) has been cut in two places. Above, where it is emerging from the under surface of the occipito-sphenoid pro-cartilage; and below, where it traverses the centra of two of the upper cervical vertebrae. A dark area just behind the upper section of the notochord probably indicates the centrum of an occipital vertebra.

which become grouped together so as to form the hypoglossal nerve. These nerves, considered from the phylogenetic standpoint, are anterior to the first spinal nerve of the frog which is distributed to the tongue. This nerve is probably composite in nature and represents spinal nerves which are more posterior in position than the nerves that give rise to the hypoglossal nerve in mammalia. At the junction of any two regions of the vertebral column, a modification of the vertebral elements takes place in adaptation to the requirements of the particular regions considered and the intermediate forms

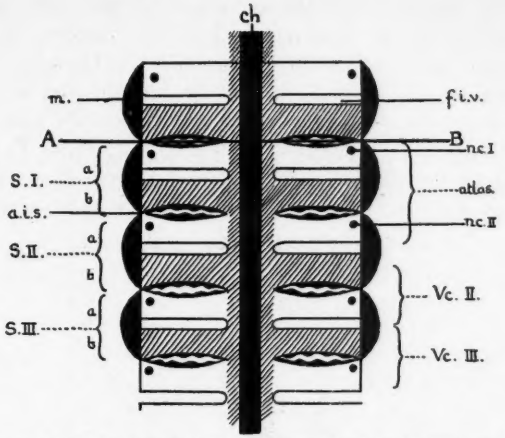

Fig. 10. Diagram indicating the position of the cranio-vertebral boundary (after Barge).

ch.	Chorda dorsalis.	*nc. I.*	First cervical nerve.
M.	Myotome.	*nc. II.*	Second cervical nerve.
A.B.	Cranio-vertebral boundary.	*Vc. II.*	Second cervical vertebra.
S.I., S.II., S.III.	First, second and third spinal sclerotomes.	*Vc. III.*	Third cervical vertebra.
		f.i.v.	Fissura intervertebralis (v. Ebner)
a.	Cranial semi-segment.	*a.i.s.*	Arteria interprotovertebralis.
b.	Caudal semi-segment.		

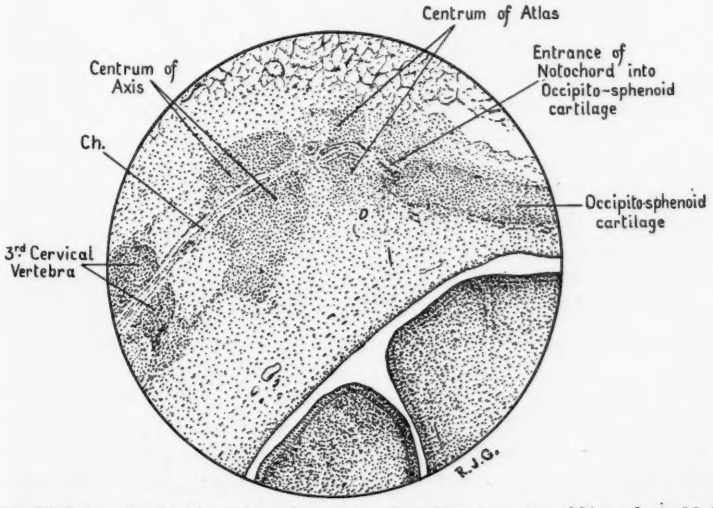

Fig. 11. Median sagittal section through occipito-odontoid region of a rabbit embryo 16 days (10 mm.). The notochord (*Ch.*) is seen traversing the cartilaginous body and odontoid process of the axis, it then passes through a dark area which probably corresponds to the centrum of the last occipital vertebra; it subsequently enters the dorsal aspect of the occipito-sphenoid cartilage and reappears on its ventral aspect in the roof of the pharynx.

of vertebrae are spoken of as transitional or passage vertebrae, as is the case in the fifth lumbar and seventh cervical vertebrae in the human subject. In the occipital region the atlas may be regarded as a transitional vertebra which has been modified by the separation of its centrum, which has become fused with the body of the axis to form the odontoid process. The hypochordal arch which is rudimentary (see fig. 9) in the vertebrae posterior to it, is strongly developed in the atlas so as to form the anterior segment of the ring which encloses the odontoid process. And the spine of the neural arch has been suppressed so that it will not impede rotation of the atlas upon the axis. In the early stages of development the skeletogenous tissue of the vertebral

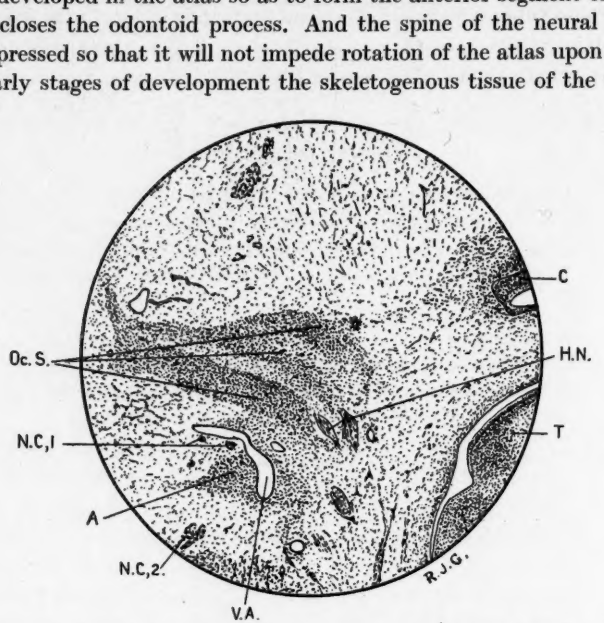

Fig. 12. Sagittal section to one side of the median plane of the occipito-cervical region of a 12 mm. human embryo showing occipital sclerotomes and atlas.

A.	Atlas.	*N.C.* 2.	Posterior division of second cervical nerve.
Oc.S.	Occipital sclerotomes.	*V.A.*	Vertebral artery.
H.N.	Roots of hypoglossal nerve.	*C.*	Cochlea.
N.C. 1.	Posterior branches of suboccipital nerve.	*T.*	Tongue.

column and the cranium are continuous with one another and a distinction between hypoglossal sclerotomes and cervical is not so clear as at a later stage when chondrification and ossification have taken place. Further no sign is present of the articulations between the condyles of the occipital bone and the atlas and it is not until a comparatively late period (in the sheep 16 mm. stage, Barge), that the position in which this joint is going to form can be distinguished. The hypoglossal sclerotomes fuse together to form the occipital plates or "pillars." This fusion varies in the completeness with which the last hypoglossal sclerotome is joined to the more anterior sclerotomes, and hence the occasional appearance, as an abnormality, of what is termed an

occipital vertebra. It will thus be apparent that a manifestation of an occipital vertebra is due to an incomplete assimilation of the last hypoglossal sclerotome into the skull.

What appears to be an incomplete assimilation of an occipital vertebra, similar to that which occasionally occurs in the human subject, is the normal condition in some types of mammals, e.g. among the carnivores, the Wolverine or Glutton (*Gulo luscus*), and the Red Coati (*Nasua rufa*) of South America. In both these types which are nearly related, and belong to the Weasel tribe or Mustelidae, there is a distinct appearance of an occipital vertebra which projects in relief round the margin of the foramen magnum.

ETIOLOGY OF CONGENITAL VARIATIONS IN THE CRANIO-VERTEBRAL AND OTHER REGIONS

As the result of the examination of a considerable number of specimens of congenital variations in the occipito-atlantal region, and of variations and abnormalities occurring elsewhere in the vertebral column and skeleton, we have been impressed by the frequency with which these variations are attended by:

1. Asymmetry.
2. Irregularity and roughness of the bony surfaces.
3. Alterations in form, which in some cases appear to be the result of intrauterine pressure.
4. Defects of development, which may be limited to the part concerned, e.g. failure in the union of the two halves of the neural arch of an atlas fused with the occipital bone; or may occur in other parts of the body, e.g. fusion of other vertebrae in the spinal column, Specimen 1, Moreover the defects in the development of the vertebral column may be associated with other anomalies of a different nature as in a case described by Dr G. H. Edington, in which "Multiple Malformations" (Genito-urinary and Skeletal) occurred on the right side of the body in an infant who died after operation for Atresia Ani. The skeletal defects consisted of fused ribs; the stump of a cervical rib on the right side; two cervical ribs on the left side; asymmetry of the sternum; deficiency of laminae and transverse processes of the vertebrae on the right side, with fusion of individual bones; absence of the right half of the body of the 5th dorsal vertebra, causing spinal curvature; dwarfing of the right thumb and corresponding metacarpal bone; hare-lip on the right side, and absence of the right kidney and ureter.

Also in a case which has previously been described by one of us (R. J. G.), an atlas showing marked asymmetry and irregularity was fused with an imperfectly assimilated occipital vertebra, and in the same subject there was a pair of unequally developed cervical ribs.

Similar cases of multiple anomalies of the vertebral column, including synostosis of the atlas with the occipital, fusion of two or more vertebrae with one another, great irregularity and asymmetry associated with the

presence of cervical ribs, have been described by Barclay-Smith, Brash, and Goodhart and one by Rokitansky in which the vertebral anomalies were associated with 14 pairs of ribs.

These cases of multiple variations clearly indicate a disturbance of the normal developmental processes, and the irregularity, asymmetry and occasional association of other anomalies, with a "liberated occipital vertebra"

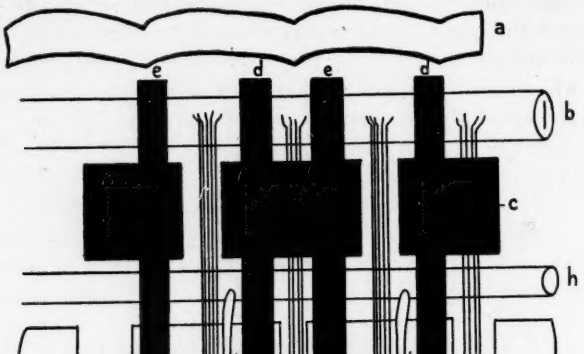

Fig. 13. Diagram after Primrose of the arrangement of somatic arches in relation to vertebrae and myotomes with segmental arteries and nerves.

a. Skin.
b. Dorsal nerve tube.
c. Vertebral bodies.
d. Anterior neural arches of vertebral relation.
e. Posterior neural arches of vertebral relation.
f. Dorsal, or sensory nerves passing in sclerotomes to the skin.
g. Ventral, or motor nerves passing to the myotomes.
h. Aorta.
i. Segmental arteries.
j. Myotomes, intervertebral in position.
k. Sclerotomes.

or "fused atlas," appear to indicate that these variations are not rightly regarded as a regressive or progressive tendency in phylogeny, but are rather the result of a morbid condition interfering with the normal development of the foetus, and akin to the conditions which give rise to such defects in development as spina bifida agnathia, or cyclops; namely a degenerate or

diseased condition of either parent causing a diminished vitality of the germinal cells or imperfect nutrition of the foetus due to a weak or diseased state of the mother, or in a non-placental animal to the action of a deleterious environment on the growing embryo or larva. Many of these variations however cannot be classed as a mere defect or arrest of development, there is sometimes the formation of an additional part, such as a cervical rib or supernumerary digit; and it seems probable that a weakening of the normal tendency in heredity of the parental stock to produce like offspring, has taken place, and that an unstable condition in the development of the foetus or larva is produced which induces variations apart from, or in addition to, imperfections in growth due to simple arrest of development.

This conception has to a certain extent been foreshadowed in our previous publications (11, 12), and those of Tornier, who has independently come to the conclusion that a weakening of the germ-cells may result in defects of development which may be inherited. Tornier's deductions were founded on observations upon the deleterious effects of unhygienic conditions on the larvae of gold fish, the various fancy-types of which, namely the "veil-fish," the "bull-head," and "telescopic-eyed-fish," are degenerate derivatives of the wild grey carp. The pigment in some of these types has been reduced to such an extent that a condition of albinism is developed, which like albinism in other classes of animals may be inherited. These inherited defects of development occur frequently in other classes of domesticated animals, e.g. the shortened "muzzle" of the Pekinese dogs, pugs, and bull-dogs, and of the domesticated pig. We believe, however, that unhygienic conditions affecting the parental stock and weakening the germ-cells, may induce not only defects in development, but also actual variations, owing to an interference with the hereditary power of the embryonic cells to carry out their normal function of building up the embryo on similar lines to the parental stock. In other words *an unstable condition is induced due to a weakening of this hereditary power*, apart from mere inability to complete the normal processes of ontogeny, e.g. the union of the palatal processes to form the roof of the mouth.

In conclusion we may again refer to the primary conditions which have determined the formation of a moveable joint at the junction of the head and vertebral column. Also to the probability that this joint is not formed in the same situation in all types of animals, but that, in the mammalia its position is remarkably constant and is developed as has been shown by Barge in the sheep and human subject between the caudal segment of the last hypoglossal sclerotome and the cranial segment of the first spinal sclerotome.

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IS THE RAMUS OPHTHALMICUS PROFUNDUS THE VENTRAL NERVE OF THE PREMANDIBULAR SEGMENT?

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The ramus ophthalmicus profundus is one of three nerves that may arise, in fishes, from the profundus ganglion, the other two being the portio ophthalmici profundi and the radix longa.

The portio ophthalmici is distributed to that part of the dorsal surface of the head that lies between the alisphenoid cartilages of opposite sides, and as these cartilages are dorsal cartilages related to the premandibular segment (see Allis, 1923), the portio ophthalmici is quite certainly a dorsal nerve, and as such it must have lain, primarily, in the septum between the premandibular and mandibular segments.

The radix longa runs outward to the ciliary ganglion, and the ciliary nerves, which arise from the latter ganglion, are distributed to the eyeball, thus not being, in distribution, either typically dorsal or ventral.

The ramus ophthalmicus is distributed largely to the dorsal surface of the snout, that is to tissues, including the nasal capsule, that lie at the anterior end of the trabecula, the latter cartilage being the pharyngeal element of the premandibular arch (Allis, 1923). The nerve might therefore be, from its course and distribution, either a lateral or a ventral one, but as it is said to contain no latero-sensory or communis fibres, it cannot be a ramus lateralis. Of the nerve in *Petromyzon planeri*, Koltzoff says (1902, p. 518) that although no ramus ventralis is developed in relation to the profundus ganglion, "Ebenso giebt es keine Möglichkeit zu bestimmen ob der N. ophthalmicus profundus einen dorsalen oder einen ventralen Ast, oder beide zusammen, vorstellt."

The ganglion of the profundus lies, in *Petromyzon planeri*, in the septum between the first and second somites (Koltzoff, 1902), and this must be its position in other fishes also, for Guthke says (1906, p. 31) that, in Torpedo, the upper end of the mandibular (second) somite lies between the profundus and trigeminus ganglia. It is generally conceded that this ganglion belongs to a segmental nerve lying next anterior to the trigeminus, and hence related to the premandibular segment. Such being the case, the ramus ventralis of this segment, if there were such a nerve, would, when the pharyngeal element of the arch (trabecula) swung upward and forward from a position perpendicular to the notochord to one parallel to it, be pulled forward and upward to a greater or lesser extent across the external surface of the premandibular somite. It would therefore lie dorsal to certain of the muscles later developed from that somite, and hence dorsal also to those branches of the nervus oculo-

motorius that innervate them, and this is what is actually found in the adults of all vertebrates, for the ramus ophthalmicus profundus always passes dorsal to the inferior division of the nervus oculomotorius, and, in the Petromyzontidae, dorsal also to the superior division of that nerve (Fürbringer, 1875; confirmed by me in *Entosphenus tridentatus*). In the Elasmobranchii the nerve apparently crosses the external surface of the premandibular somite at a lower level than it does in the Teleostomi, thus leaving a larger part of the somite dorsal to the nerve, this perhaps in a measure accounting for the fact that in the former fishes the superior division of the oculomotorius innervates two recti muscles developed from the premandibular somite, while it innervates but one in the Teleostomi.

The relations of the ophthalmicus profundus to the nervus oculomotorius thus being accounted for, it remains to consider its relations to the nervi opticus and trochlearis, and Koltzoff's (1902) descriptions of Petromyzon are best adapted to this purpose. The optic vesicle lies, in early stages of the latter fishes, actually anterior, but morphologically dorsal or dorso-anterior to somite I; as shown in Koltzoff's Reconstruction VIII. The ectodermal thickening that gives origin to the optic lense is not shown in this reconstruction, but in the next following one of the series it is shown lying directly between the first and second somites, in the horizontal line of the epibranchial ganglia, and von Kupffer (1895) says, rightly or wrongly, that it is actually the anterior one of those ganglia. The optic vesicle and the placode of the lense are thus separated from each other by a considerable interval in these early stages, and the optic vesicle is shown growing toward the lense and crushing somites I and II considerably out of place. If the ramus ventralis of the premandibular arch crossed the external surface of somite I, as just above suggested, the optic vesicle, in order to reach the lense, would have to pass internal to this nerve, and the nerve would therefore ultimately lie dorso-anterior to the nervus opticus, as the ophthalmicus profundus actually does.

The musculus obliquus superior is said to be derived from an anterior prolongation of the dorsal portion of the second (mandibular) somite, which grows forward dorsal to somite I. As this portion of the somite grew forward, it would pass dorsal to both the dorsal and ventral roots of the nerve of the next anterior (premandibular) somite, and internal to the rami dorsales of those two roots. To reach the eyeball the muscle would then have to pass outward anterior to the ramus dorsalis of the premandibular segment, and would lie between that ramus and the ramus ventralis when those two nerves became inclined forward in connection with the cranial flexure and the swinging upward and forward of the trabeculae. The muscle is innervated by the nervus trochlearis, and if this nerve followed the same path as the muscle it innervates, which seems practically certain, it would lie between the rami dorsalis and ventralis of the nervus profundus; and that is the relation it actually has to the portio ophthalmici and ramus ophthalmicus of that nerve. If the ramus ophthalmicus were a ramus dorsalis, the adult conditions could

only be explained by the assumption that the obliquus superior and the nerve that innervates it either passed outward between two branches of the ramus dorsalis of the nervus profundus, or that the muscle passed outward anterior to both those branches and the nerve that innervates it between them; either of which assumptions seems improbable.

The definitive conditions in the adults of fishes thus all favour the assumption that the ramus ophthalmicus profundus is a ventral nerve, and if this be so, the preauditory nerves, as well as the preauditory arteries and cranial cartilages, show that there are, in the vertebrate head, persisting portions of a visceral arch related to the first, or premandibular somite. There are, however, no indications that I can recognize of other, more anterior arches. Von Kupffer (1894) describes two premandibular arches in *Ammocoetes planeri*, and calls them the trabecular and palatine arches, the trabecular lying anterior to the palatine. These two arches and the mandibular arch are all said to arise in connection with a single large evagination of that part of the gut that lies anterior to the bottom (fundus) of the stomodaeum, and that is accordingly considered by von Kupffer to represent the preoral gut. The related visceral pouches are angular projections of this large preoral evagination, and are shown as distinctly separate in a six day embryo. In a seven to eight day embryo the palatine and mandibular pouches have partly fused with each other, having but a single common stalk, and in a 4 mm. embryo they have completely fused. Tissues said to represent the trabecular and palatine arches are shown lying posterior to their respective pouches in a six day embryo. In a seven to eight day embryo tissues said to represent these two arches and the mandibular arch are shown, and the trabecular and palatine arches have here fused to form a single mass. Three arterial vessels are described, and they are all considered by von Kupffer to represent aortic arches. In a figure showing a horizontal section through the head of a 4 mm. embryo of this fish, one of these arteries lies anterior to the trabecular pouch, and hence has not the relations of an aortic vessel to either of the three arches here described. The second artery lies between the trabecular and palatine pouches, directly internal to the trabecular arch, and hence has the relations to it of an aortic arch. The third artery lies latero-posterior to the tip of the mandibular pouch, directly internal to the hind end of the palatine arch, and hence actually between the palatine and hyal pouches. It is, however, said to be the mandibular aortic arch, because of its position directly anterior to the hyal pouch, and it is quite certainly that aortic vessel. The next anterior artery is then the premandibular aortic arch, and the so-called trabecular arch to which it is related must be the premandibular arch. There is no visceral arch anterior to this one. The anterior one of the three arteries described by von Kupffer cannot therefore be an aortic vessel, and comparison with Cori's (1906) descriptions shows quite conclusively that it is some part of the arteria cerebralis. Von Kupffer says (1894, p. 35) that the lateral dorsal aorta (Aortenwurzel) takes up a vessel

"*v*" which lies along the side of the brain and dorsal to the eye, but in his transverse sections this vessel is shown in exactly the position of the vena capitis lateralis of Cori's descriptions; and it is quite certainly that vessel, and not an artery.

Von Kupffer denies the presence of somites in the preoral region, and derives the eye muscles from the endodermal tissues of his trabecular and mandibular evaginations, the palatine evagination, which has fused with the mandibular one, doubtless also contributing to their formation. The trabecula is said by him to be differentiated from the dorsal end of the trabecular evagination, to extend forward as far as the optic chiasma and posteriorly as far as the parachordal, with which it fuses. The trabecula is thus, in his opinion, of lateral-plate and not of somital origin, which is in accord with my conclusions. Koltzoff says (1902, p. 367) that the trabecula of these fishes is developed from the first sclerotome, and the "anterior parachordal" mainly from the second but partly also from the third sclerotome (*l.c.* p. 336), the latter cartilage doubtless corresponding to that anteriorly projecting portion of the parachordal of certain fishes that represents the polar cartilage. Koltzoff says (*l.c.* p. 354) that there is no definite mark between the somites and the lateral-plates, and that "man müsste so die Sklerotome bald zu Somiten, bald zu Seitenplatten rechnen." His work is thus in no way opposed to the view that the polar and trabecular cartilages are of lateral-plate and not of somital origin. The so-called anterior head cavity would doubtless represent a part of the lateral-plate of the premandibular segment, as certain authors have suggested.

If the foregoing conclusions are correct, and also those set forth in certain of my earlier works (Allis, 1918, 1919, 1922 *a*, 1923), it is evident that the preauditory portion of the skull of vertebrates, like the postauditory portion, is of segmental origin, but that it contains both vertebral and visceral-arch components instead of vertebral ones only. The following deductions therefore seem warranted:

1. The side walls of the chordal portion of the myodome are formed by ventral vertebral arches similar to those found on the vertebrae of the trunk.

2. The pituitary veins traverse the prechordal portion of the myodome and therefore form a prevertebral commissure connecting the venae capites mediales of opposite sides. That part of each of the latter veins that lies anterior to this point runs proximally (upward) along the trabecula (pharyngopremandibula), and is therefore a vessel related to the premandibular arch.

3. The lateral dorsal aorta of either side runs forward, as the internal carotid, along the lateral wall of the myodome, and enters the prevertebral portion of that chamber. There it may fuse with its fellow of the opposite side (Teleostei), but this fusion is a secondary one (Allis, 1919), the primary fusion of the vessels of opposite sides apparently taking place in the cranial cavity between the posterior cerebral arteries.

4. The orbito-nasal artery of the Teleostei and Crossopterygii has an

origin from the internal carotid (lateral dorsal aorta) and relations to the trabecula that suggest an arterial vessel related to the premandibular arch. This artery is not found in the Elasmobranchii (Allis, 1908, p. 119), and is doubtless there replaced by the suborbital branch of the piscine external carotid. The anterior cerebral artery is a dorsal branch of the internal carotid, and the fact that it runs upward posterior to the nervus opticus and then sends branches to the olfactory lobe and nerve favours the view that the nervus opticus lay primarily anterior to the nervus olfactorius.

5. The suborbital latero-sensory line is a descending line in the mandibular arch, similar to the hyomandibular line in the hyal arch, as I have previously suggested (Allis, 1922 *b*). The anterior (morphologically ventral) portion of the line, which is infranasal in position, has acquired secondary relations to the premandibular arch (trabecula), just as the ventral end of the hyomandibular line acquires secondary relations to the mandible.

6. The anterior head line of pit organs and the supraorbital canal line are both innervated by the ramus ophthalmicus superficialis lateralis, and in certain fishes they appear as a single continuous line while in others they are wholly independent of each other. Both lines are directed morphologically dorsally, and this suggests that they may have been primarily independent, one related to the mandibular and the other to the premandibular segment. The innervation by a nerve that apparently belongs to the trigeminus seems unfavourable to this view, but as each of the two lines, if primarily independent, would have been innervated by a dorsal branch of the nerve of its own segment, those two dorsal branches might readily have fused with each other by one or the other slipping over the top of the parasphenoidal leg of the alisphenoid, which, when present, always forms the anterior boundary of the foramen trigeminum. In favour of such a fusion of these two nerves is the fact that the ophthalmicus lateralis almost invariably issues from the skull through a foramen that lies considerably dorso-anterior to the foramen trigeminum, and that it is joined, in certain fishes, not only by fibres derived from the trigeminus ganglion (ramus ophthalmicus superficialis trigemini) but also by fibres derived from the profundus ganglion (portio ophthalmici profundi).

7. The supraorbital canal runs dorso-anteriorly, following the curved and inclined course of the alisphenoid cartilage of selachian embryos, and on reaching the anterior end of the snout either ends there (certain of the Teleostomi), or turns posteriorly to either end between the nasal apertures (certain others of the Teleostomi) or to reach and fuse with the anterior end of the suborbital canal (Selachii). If this canal is a dorsally directed head line, as above suggested, this curved course of the canal, which has heretofore seemed to me inexplicable, is easily accounted for as a result of the cranial flexure and its subsequent reduction, and the potential anterior end of the canal would lie, morphologically, anterior to the nasal pit.

8. Let it be assumed that the supraorbital canal is the premandibular

head line, as above proposed. The nasal sense-organ must then have lain, primarily, posterior to this line, somewhere between it and the middle head line, which is innervated by the nervus glossopharyngeus. There is no dorsal head line related to the hyal arch and innervated by the nervus facialis. Is it therefore possible that the nasal sense-organ represents this missing line? If so, it would lie approximately in the region recently assigned to it by Kingsbury and Adelmann (1924); and that the nasal organ is of latero-sensory (nerve-hillock) origin has been both suggested and contested. In favour of its latero-sensory origin is the well-known manner in which the nasal pit becomes enclosed in the Teleostomi, and it is to be especially noted, in this connection, that the nasal pit becomes definitely enclosed only in those fishes (Teleostomi) in which the latero-sensory canals are formed by the meeting and fusion of their lips directly above the enclosed organs. When the canals are developed as they are in the Plagiostomi (Allis, 1922 *b*), the primitive pores lying directly above the latero-sensory organs, the lips of the nasal pit may meet and overlap, but they never fuse. And the same is true of the auditory organ, for the endolymphatic duct remains open in the Plagiostomi, but is always, so far as I know, closed in the Teleostomi. The invagination and enclosure of both the olfactory and auditory organs of a given fish thus correspond to the invagination and enclosure of its latero-sensory organs. This has never heretofore been noted, and it would seem to be a striking example of the persistence of an ancestral characteristic. The nasal sensory tissue and its related nerve would, under this assumption, simply have been carried forward by the cranial flexure to their present actual positions and then have remained there when the cranial flexure was reduced, the organ then undergoing a change of function; and such a shifting of this tissue and nerve might, perhaps, have been the cause of the exceptional course of the nervus trochlearis.

PALAIS DE CARNOLÈS
MENTON
September 27th, 1923

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DEATH OF PROF. JOHN IRVINE HUNTER

Just as this number of the Journal goes to press we learn with the deepest regret of the death in London of PROFESSOR JOHN IRVINE HUNTER, Challis Professor of Anatomy in the University of Sydney. British Anatomy has lost, at the early age of 27, her most promising recruit.

REVIEW

The Morphology and Evolution of Apes and Man. By Dr CHARLES F. SONNTAG. pp. xi + 364. 57 figures in text, one of them a phylogenetic tree of the Primates. (London: J. Bale, Sons and Danielson, Ltd. 1924.) Price 12*s.* 6*d.* net.

It is unnecessary to introduce Dr Charles F. Sonntag to the readers of this *Journal*; he is well known to members of the Anatomical Society and to Fellows of the Zoological Society as a contributor to their *Proceedings*. As Prosector to the Zoological Society, as successor to Garrod, Beddard and Wood-Jones, he has a wealth of new material at his disposal and has taken advantage of his opportunities to investigate the anatomy of the Primates—particularly of the Anthropoid apes. His recent papers on the nervous, vascular and muscular systems of these animals are well known. In the present work he surveys the anatomical characters of all members of the Order Primates, including in this order the great variety of forms which lie between the lowest kinds of Lemurs and the highest types of man. Much of what he has to tell is based on first-hand information.

Prof. G. Elliot Smith has written a Foreword, from which we learn how Dr Sonntag came to write this book and the object which he had in view. "Some time ago," writes Prof. Elliot Smith, "I ventured to suggest to him (Dr Sonntag) that he could render an invaluable service to students and investigators if he would prepare and publish full accounts of the anatomy of Anthropoid apes based upon his personal observations, with such comparative and bibliographical notes as would make his report a standard work of reference for anthropologists and anatomists. This book represents the realization of that scheme."

There is no doubt that Dr Sonntag has rendered a real service to both student and expert by placing at their disposal a text-book on the anatomy of the highest order of mammals. Its defects are those of its author's great modesty. Prof. Elliot Smith rightly commends "its freedom from the bias which writers intent upon the interpretation of evidence, rather than the collection of evidence itself, are apt to introduce into their reports, however much they may strive to be impartial." Yet we could wish that its author had aimed at playing the part of interpreter as well as collector, for a text-book which presents students with a bare narration of facts is also apt to nauseate them. Nevertheless anatomists will thank Dr Sonntag for his labour, particularly for the full bibliography he has appended to his book and for the indications he has given to sources of information on each subject dealt with in his text.

ON THE AUTOSTYLISM OF DIPNOI AND AMPHIBIA

By F. H. EDGEWORTH, M.D.

Though the genealogies and affinities of Dipnoi and Amphibia have been much discussed, the particular problem of the derivation and possible genetic relationship of their autostylism and more or less marked monimostylism has received little attention.

The subject has been discussed from two points of view, firstly as a problem which affects each group separately, and secondly as one which is common to both groups.

The autostylic and monimostylic condition of the jaw-apparatus of Dipnoi was considered to be secondary by Huxley, Dollo, Bridge, Goodrich, and Luther. On the other hand, K. Fürbringer stated that it was not proven that their autostylism was derived from a hyostylism, and was of opinion that the primitive condition was one in which the mandibular and hyoid bars articulated separately with the cranium.

Of these authors only Luther took account of the mandibular muscles, and he suggested that a Levator maxillae superioris s. Constrictor i. dorsalis disappears.

The autostylic and mostly monimostylic condition of Amphibia was not considered by Semon, Assheton, and Kerr; it was thought to be secondary by Huxley, Dollo, Pollard, and Luther; and was held to be primary by K. Fürbringer.

The majority of these observers did not take the mandibular muscles into consideration, but Pollard thought that a Levator maxillae superioris disappears, and Luther put forward the theory stated below.

According to Dollo and Bridge the conditions were separately acquired in Dipnoi and Amphibia. Dollo thought that the condition in Dipnoi was an adaptation to a "régime tritateur," but in criticism of this opinion Bridge stated that such an explanation would not apply to Amphibia, and he also pointed out some resemblances between the larval Anuran condition and that of Marsipobranchii.

Huxley, Semon, Assheton, Kerr, and Boas did not discuss the problem.

Sewertzoff stated that the early stages of Ceratodus and Amphibia (especially Urodela) are very similar, whilst the later stages diverge. K. Fürbringer considered that the Amphibian condition was derived from a Dipnoan one. Versluys, who discovered the Levator quadrati of Gymnophiona, held that their streptostylic condition is primitive. This theory was developed by Luther, who stated that the semi-streptostylic condition of some Urodela,

e.g. *Hynobius, Salamandrella,* is also a primitive one. He therefore rejected the theory of K. Fürbringer and held that, in any discussion of the relations of Amphibia and Dipnoi, features which are related to their autostylism must be left out of account.

In a paper published in 1911 I stated that the primordium of the masticatory muscles of *Scyllium, Acipenser, Lepidosteus, Amia* and *Salmo,* separated into an upper portion—the Constrictor i. dorsalis or its homologues—above the palatopterygoid process of the Quadrate, and a lower portion—the Adductor mandibulae or its derivatives—extending from that process to the Mandible. I also stated that the Levator bulbi of *Rana* is given off from the upper surface of the Levator mandibulae anterior, and did not regard it as homologous with the Constrictor i. dorsalis of Selachii and Teleostomi; nor did I recognise a Constrictor i. dorsalis in *Triton, Necturus* and *Ceratodus,* and regarded its absence as a primitive feature. I consequently looked upon the monimostylic condition of Amphibia and Dipnoi as primary, and the streptostylic condition of Selachii and Teleostomi as secondary, developed in correlation with a division of the primordium of the masticatory muscles into upper and lower portions, above and below the palato-pterygoid process of the Quadrate.

The primordia of the Obliquus superior and Rectus externus in Selachian embryos were looked upon as merely anterior projections from the upper ends of the mandibular and hyoid muscle-plates to form these muscles, i.e. I doubted the v. Wijhe doctrine, and it was considered that the ocular musculature was primarily formed solely from the premandibular somite.

These views have not passed unchallenged. Luther, in 1914, gave a full account of the mandibular muscles of Amphibia. In this valuable paper he came to the conclusion that the Levator quadrati and Compressor glandulae orbitalis of Gymnophiona, and the Levator bulbi of Urodela and Anura are the homologues of the Constrictor i dorsalis of Selachii and Teleostomi, and that the other masticatory muscles of Amphibia are (collectively) the homologues of the Adductor mandibulae of Selachii and Teleostomi.

In support of these conclusions he advanced the following arguments. The Levator quadrati of Gymnophiona closely resembles the Constrictor i. dorsalis in origin and insertion, only differing in that its origin is rostral (anterior) to the trigeminal foramen whereas that of the Constrictor i. dorsalis is caudal (posterior) to it. This difference is due to a forward shifting of the origin of the muscles in Gymnophiona. The Levator quadrati of Gymnophiona also, as Versluys recognised, corresponds with the Protractor pterygoidei of Saurii in position and derivation, and is certainly homologous with it. Further, there is a similarity in the proximal nerve supply of the Levator quadrati and Constrictor i. dorsalis—the nerve of the former coming from the Ganglion Gasseri in *Siphonops,* that of the latter coming from V_3 very high up. Among Salamandridae are forms, e.g. *Hynobius* and *Salamandrella* which possess a very moveable Quadrate and in which a part of the lateral fibres of the Portio

sagittalis of the Levator bulbi shows many similarities to and is homologous with the Levator quadrati of Gymnophiona.

Ontogenetically, in *Rana* and *Pelobates*, all parts of the Levator bulbi are derived from a single Blastema, indicating a single genesis of the whole muscle. This Blastema is differentiated from the tissue lying dorsal to the Adductor, and there is no connection between it and the Adductor. The statements of Edgeworth in regard to the origin of the Levator bulbi of *Rana* might be explained by the lateness of development, for the muscle only functions after metamorphosis, and the whole difference between Selachii, Ganoids, Teleostei, and Sauropsida, on the one hand, and Amphibia on the other, be a mere matter of the time of division.

The nerve-supply of the Levator bulbi is derived in some cases from V_1, in others (Anura) from V_1 and V_2, in others again (Amphiumidae) from the N. pterygoideus V_3. This variation in the course of the nerve-fibres does not militate against the theory.

In view of this diversity of opinion the subject has been reinvestigated with the results described below. I may perhaps anticipate the conclusions by saying that all the additional evidence I have been able to collect supports the opinion I previously published. It is sub-divided as follows:

1. The skeletal evidence.
2. The evidence derived from the development of the masticatory muscles.
3. Relationship of the Quadrate and masticatory muscles of Elasmobranchii and Teleostomi to those of Dipnoi and Amphibia.

Skeletal Evidence

Dipnoi. The development of the Quadrate of *Ceratodus* has been described by Sewertzoff (1902), Greil (1913), and myself (1923). It is developed as an independent mass, which becomes fixed to the Chondrocranium by ascending, otic, and basal processes. The development of the Quadrate of *Lepidosiren* was described by Agar, who stated that the rudiment of the Quadrate is from the first continuous with the Trabecula by the Processus basalis. A strand of dense connective tissue connecting the distal end of the rudiment of the Quadrate with that of the palatine tooth probably represents the vestige of the pterygoid process. The otic process fuses with a shelf which is formed as an anterior continuation of the side wall of the auditory capsule. It is not possible to speak of a Processus ascendens as distinct from the basalis.

Urodela. In a 11 mm. larva of *Amblystoma punctatum*, according to Winslow, the ascending process of the Quadrate is fused with the trabecular crest, and the otic process has begun to develop. This process is longer in a larva of 12 mm. In a larva of 39 mm. the otic process has fused with the otic capsule, whilst the pterygoid process passes forward from the point where the ascending process joins the body of the Quadrate and ends free, just below the ventro-median surface of the eye. The basal process is formed by fusion of the

dorso-median surface of the body of the Quadrate with the margin of the basilar plate. In a young animal of 69 mm.—in which the gills have atrophied —the condition is similar except that the pterygoid process passes forwards and outwards.

I find that in a larva of 13·5 mm. (fig. 41) the ascending and otic processes have fused with the trabecular crest and the auditory capsule respectively. The chondrified base of the pterygoid process is continued forwards as a thin column of cells the anterior end of which is continuous with the Trabecula. In a larva of 18 mm. the anterior cellular part of the pterygoid process has atrophied and the front end of the posterior part lies above the pterygoid part of the (as yet undivided) pterygoid-palatine bone. In a larva of 27 mm. the basal process is united with the margin of the basilar plate—as described by Winslow in the 39 mm. larva.

Larvae of *Amblystoma tigrinum* show similar conditions.

In *Triton* larvae, according to Gaupp, the Quadrate is formed independently of the Chondrocranium and fuses with it by ascending, otic, and basal processes. The basal process fuses with the ventral surface of the auditory capsule just where this unites with the basal plate. The pterygoid process, developed last, lies on the earlier-formed pterygoid bone, and has a pointed free extremity.

Peters (1910) stated that the basal and otic processes do not fuse, cartilaginously, with the auditory capsule, nor in *Siredon*, as far as his observations went—greatest length of larvae investigated 25 mm.—nor in *Necturus*.

In a larval *Triton cristatus*, however, of 33 mm. I find a complete cartilaginous continuity of the otic and basal processes with the auditory capsule.

The Quadrate in *Salamandra atra* is very similar to that of *Triton cristatus*.

In the adult state of *Desmognathus fuscus*, according to Wiedersheim, the Quadrate has two cartilaginous ends, "welche die prootische Gegend von unten und aussen umgreift." He also depicted a pterygoid process with a free anterior extremity.

I find that in a larva of 19 mm. (fig. 42) the Quadrate, which is oblique in position, has four processes. The pterygoid process is wholly cellular, and passes from the Quadrate to the Trabecula; the ascending process is continuous with the trabecular wall, the otic process is continuous with the outer wall of the auditory capsule, and the basal process is continuous with the inner part of the floor of the auditory capsule. There is only a short larval stage. In an adult of 35 mm. the conditions are similar except in regard to the pterygoid process, the anterior part of which has disappeared, and the now chondrified posterior part ends free, ventro-lateral to the eye.

The Quadrate of *Spelerpes* was not described by Wiedersheim. In a 25 mm. larva the Quadrate has pterygoid, ascending, and otic processes, but as yet no basal process. The pterygoid process is wholly cellular, its anterior end is continuous with the Trabecula. The cartilaginous ascending process is continuous with the trabecular wall, and the cartilaginous otic process is continuous with the outer wall of the auditory capsule. In a larva of 36 mm. the Quadrate

has become oblique in position, sloping downwards and forwards. Chondrification has spread a little way along the pterygoid process. A basal process has developed and connects the Quadrate with the inner part of the floor of the auditory capsule. In an adult, of 49 mm., the conditions are similar, except that the anterior part of the pterygoid process has disappeared.

In the adult stage of *Plethodon glutinosus*, according to Wiedersheim, the pterygoid process of the Quadrate ends free, there is a basal joint, and the otic process is continuous with the auditory capsule. No statement was made in regard to the ascending process.

Plethodon cinereus is hatched in the adult state, measuring about 20 mm. There is no free-living larval stage. In a specimen measuring 25 mm. (fig. 43) the Quadrate is in an oblique position, sloping downwards and forwards, its pterygoid process ends free, the ascending process is continuous with the trabecular wall, the otic process is continuous with the auditory capsule, and the basal process is continuous with the floor of the auditory capsule. In a specimen of 49 mm. (fig. 44) the conditions are similar except that there is a band of closely aggregated cells across the basal process—the commencement of the basal joint.

In the first larval stage of *Amphiuma tridactylum* investigated by Winslow the Quadrate has an ascending process which joins the trabecular crest and a slender stapedial process which passes backwards and joins the small stapes; whilst in the second stage there are, additionally, otic and basal processes which are continuous with the otic capsule. The pterygoid process passes forwards from the ventral surface of the ascending process in close proximity to the ventral margin of the Trabecula; towards its anterior end it curves laterally and broadens into an oval plate which lies a short distance posterolaterally from the base of the antorbital process. In the adult, according to Wiedersheim, the Quadrate is continuous with the basilar plate and otic capsule by basal and otic processes, whilst the pterygoid process ends above the hinder end of the maxilla.

Comparison with *Cryptobranchus* and *Menopoma* suggests that the stapedial process is to be regarded as a forward process of the stapes which has fused with the Quadrate rather than as a backward process of the Quadrate. Investigation of earlier stages would decide this question.

Descriptions of the Quadrate in *Hynobius*, *Megalobatrachus* and *Menopoma* were published in this *Journal* in 1922.

The Quadrate of the adult stage of *Salamandrella Keyserlingii* was not described by Wiedersheim. Luther stated, though without giving any details, that the skull is semistreptostylic.

I find that in a 13·5 mm. larva (fig. 45) the Quadrate has pterygoid, ascending, and otic processes. The pterygoid process is continuous anteriorly with the Trabecula, its posterior part is cartilaginous and its anterior part cellular. The ascending process is continuous with the trabecular wall, and the otic process with the auditory capsule.

In a 17 mm. larva (figs. 46–48) the basal process of the Quadrate has developed and chondrified, it extends to the floor of the auditory capsule. The other processes are as in the earlier larva, except that comparison of figs. 45 and 46 shows that chondrification has extended further forwards in the pterygoid process. In figs. 46 and 47 the anterior cellular part of the pterygoid process is not shown. The model only represents cartilage.

In a 22·5 mm. larva (fig. 49) the anterior cellular portion of the pterygoid process has disappeared. Cells have accumulated in the basal process.

In a 34 mm. larva (fig. 50) the Quadrate has become oblique in position, sloping from above downwards and forwards. A syndesmotic joint has developed in the basal process, and the monimostylic condition of earlier stages has become a semistreptostylic one.

In an adult of 105 mm. the pterygoid process of the Quadrate passes forwards and outwards and ends free beneath the outer border of the eye. The ascending process is continuous with the trabecular wall, and the otic process with the auditory capsule. In the synchrondotic basal joint, on one side, a slightly curved slit-like cavity has developed.

Wiedersheim stated that in the adult form of *Ranodon sibiricus* the pterygoid process of the Quadrate is continuous with the outer posterior extremity of the nasal capsule. He did not describe the other connections of the Quadrate, but his figure 69 shows, I think, an ascending process continuous with the trabecular wall and an otic process continuous with the auditory capsule.

I find that in a larva of 21 mm. the Quadrate has pterygoid, ascending and otic processes, but as yet no basal process. The pterygoid process is continuous anteriorly with the Trabecula, just behind the antorbital process, its posterior part is chondrified, its anterior part a cellular strand. The ascending process is continuous with the trabecular wall, and the otic process with the auditory capsule. The larva is very similar to the 13·5 mm. larva of *Salamandrella*.

In a larva of 25 mm. (figs. 51, 52) the anterior cellular portion of the pterygoid process has disappeared. The anterior end of the persisting posterior chondrified portion ends at a little distance behind the antorbital process, and is not continuous with it. A basal process has developed and connects the Quadrate with the inner part of the floor of the auditory capsule.

In a young adult 85 mm. long the ascending and otic processes of the Quadrate are continuous with the trabecular wall and auditory capsule respectively. A synchondrotic joint with a slight slit-like central cavity has developed in the basal process. The pterygoid process passes forwards and slightly outwards, but does not reach the posterior margin of the nasal capsule—there being a gap of ·86 mm. Its continuity with the nasal capsule described by Wiedersheim is thus developed during adult life.

Miss Platt (1897) stated that in a 19 mm. embryo of *Necturus* the Quadrate is fused only with the Crista trabeculae (= ascending process). In a 46 mm.

embryo a cartilaginous process, extending backwards from the ascending process, is fused with the auditory capsule (= otic process). Winslow (1898) described the otic process as being present and fused with the auditory capsule in a 21 mm. embryo. Neither observer mentioned the existence of a basal process.

I find that in a 25 mm. embryo (figs. 64, 65) the Quadrate has ascending, basal, and otic processes. The ascending process is continuous with the Crista trabeculae, the basal process is continuous with the prefacial commissure by a cellular bridge, and the otic process similarly with the auditory capsule. In a 30 mm. embryo (fig. 66) these connections have chondrified.

In *Siren*, according to Wiedersheim, the Quadrate has a slender ascending process continuous with the Ala magna, and otic and basal processes both articulating with the prootic territory. From the ascending process projects forwards a finger-like process, the extremity of which bends downwards into the orbit. The size of the specimen was not stated.

Wiedersheim doubted the homology of the above-mentioned process with the pterygoid process of other Urodeles, and suggested that it is homologous with the post-orbital process of the Quadrate of some Selachians.

Winslow, however, found in *Amphiuma* and *Amblystoma* that the pterygoid process projects forwards from the base of the ascending process and not from the body of the Quadrate. I found the same condition in larvae of *Megalobatrachus* and *Menopoma*. Secondly, the post-orbital process of the Quadrate in Notidanidae is almost certainly the homologue of the otic process of Amphibia. It is thus fairly certain that the anterior process of the Quadrate of *Siren* is a pterygoid process.

A very different account of *Siren* was subsequently given by Parker, who stated that in a specimen of 13½ inches (= 34 cm.) the dorsal end of the Quadrate is "bifurcate; and both the forks are confluent with the endocranium (the trabecula and its alisphenoidal crest). The part confluent with the base is the pedicle (= basal process); that which passes into the wall is the ascending process; outside these, above, we have the otic process which is confluent with the auditory capsule and the preauditory horn." The Quadrate has "no pterygoid outgrowth and no correlated pterygoid bone." The anterior margin of the Epihyal is confluent with the Quadrate.

In a specimen from Florida 67 cm. long (about the greatest length reached by this Urodele) I find that the Quadrate is similar to that of the younger specimen described by Parker with the exception that a short pterygoid process projects downwards and forwards from the ascending process. There is no joint in the otic or basal process. The latter process is continuous with the basal plate.

Anura. In *Rana*, according to Gaupp, the Palato-quadrate develops independently of the Chondrocranium, and fuses with it by the ascending process and the Commissura quadrato-cranialis anterior. Later on, in 21 mm. larvae, an otic process is formed and fuses with the auditory capsule, and then a

pterygoid process is developed from the commissure and unites with the Processus maxillaris posterior of the Planum antorbitale. At metamorphosis the ascending and otic processes disappear, and the Palato-quadrate fuses with the Crista parotica by a new otic process. A basal process develops, abuts against, and then fuses with the floor of the auditory capsule, and a joint develops in it.

Gaupp was of opinion that the ascending and basal processes are homologous with the similarly named structures of Urodela. The otic process develops twice; of these the later one is probably homologous with that of Urodela, the earlier one being only a special provisional structure. His opinion concerning the Commissura quadrato-cranialis anterior is discussed later.

Gymnophiona. The development and adult anatomy of the Quadrate have been the object of researches by Wiedersheim (1879), P. and F. Sarasin (1890), Winslow (1898), Peter (1898), Marcus (1909), Versluys (1910 and 1912), and Luther (1914). The following is a summary of their statements. The Quadrate of *Ichthyophis* is formed as a triangular cartilage, with ascending, pterygoid, and otic processes. The ascending process becomes connected with the Taenia marginata—by cartilage according to Winslow, by connective tissue according to Peter. The otic process is only slightly marked and does not become united to the auditory capsule. The pterygoid process consists of a posterior part continuous with the Quadrate, and of an anterior part in two portions; these parts are united by cellular tissue. The Quadrate has no basal process; it has a jugal process. No mention of any process of the basal plate is made by either Winslow or Peter. On ossification, the Pterygo-quadrate is first surrounded and then replaced by bone except at its articular surfaces for the lower jaw and columella, and the upper end of the ascending process. The pterygoid process degenerates into connective tissue at the end of larval life.

In the adult the ascending process of the Quadrate passes upwards and slightly forwards along the posterior edge of the paraquadrate bone. The jugal process fills up the space between the ascending and pterygoid processes. The pterygoid process is continuous with either the pterygoid bone—in *Ichthyophis*, or with the maxillo-palatine bone—in *Caecilia* and *Siphonops* (Luther). A well-marked joint exists between the Quadrate and the basal bone in *Hypogeophis* larvae and in adult *Siphonops* (Versluys), and in *Caecilia* (Luther); whilst in adult *Ichthyophis* there is only a syndesmotic union (Luther).

In a 70 mm. larva of *Siphonops* (figs. 84–89) I find that the Quadrate has ascending, pterygoid, and jugal processes, but no otic or basal processes. There is a well-marked joint between the dorsal end of the ascending process and the upper of the two bars by which the Taenia marginata is continuous with the auditory capsule. A partially ossified process projects from the basal plate antero-laterally and then forwards, and its anterior end is continuous with the base of the pterygoid process of the Quadrate. In front of this cartilaginous continuity the now wholly ossified pterygoid process extends further forwards, and is continuous with a bone (probably the pterygoid bone) which expands into a plate lying on the upper surface of the maxillo-palatine

bone. The jugal process is the ossified anterior edge of the Quadrate and of its ascending process—not merely of the former as in *Ichthyophis*. The Columella auris abuts against the posterior surface of the Quadrate. Younger larvae were not available. Two changes take place between this late larval condition and the adult state. The joint between the ascending process and the Taenia marginata is replaced by fibrous tissue, and a joint develops between the base of the pterygoid process of the Quadrate and the process of the basal plate.

In a 28·5 mm. larva of *Ichthyophis*—rather younger than the one modelled by Peter—both the Chondrocranium and Quadrate are in a precartilaginous condition (figs. 90, 91). The Quadrate has a long pterygoid process the anterior end of which is close to but does not actually touch the Trabecula. The ascending process is continuous with the Taenia marginata. Neither otic nor basal process is present. A short process projects laterally from the basal plate, turns back, and then inwards, to join the basal plate again. (This is also shown, in transverse sections of the 35 mm. larva, figs. 100–102.) The anterior end of the Columella auris is close to the posterior end of the Quadrate.

In a 35 mm. larva (figs. 98–102) the Chondrocranium and the Quadrate with its two processes are chondrified. The changes from the earlier stages are as follows. The anterior end of the, still continuous, long pterygoid process of the Quadrate is in contact with the Trabecula (fig. 98). The upper end of the ascending process is connected with the Taenia marginata by fibrous tissue. The process of the basal plate is tied to the Quadrate by fibrous tissue (figs. 100–102). The pterygoid bone has developed; its hind end is close to the medial surface of the Quadrate.

In a larva of 59 mm. (fig. 103) the middle portion of the pterygoid process has disappeared. The anterior end of the persisting front portion no longer touches though it is close to the Trabecula; it lies on the palato-maxillary bone. The anterior end of the persisting hinder portion of the pterygoid process is ossified. The basal plate with its process, and the posterior parts of the Taenia marginata and Trabecula, have degenerated. A fibrous ligament binds the basal bone to the body of the Quadrate, its pterygoid process, and the pterygoid bone.

On comparison of the above-described phenomena it is seen that:

(1) The anterior end of the pterygoid process of the Quadrate becomes continuous with the Trabecula in *Amblystoma*, *Desmognathus*, *Spelerpes*, *Hynobius*, *Menopoma*, *Salamandrella*, and *Ranodon*. In *Hynobius* and *Menopoma* on the subsequent development of the antorbital process, the pterygoid process is found to be continuous with its inner end. This latter condition is present in the youngest available larvae of *Megalobatrachus*. In *Amblystoma*, *Desmognathus*, *Spelerpes*, *Salamandrella* and *Ranodon*, the anterior part of the pterygoid process does not develop beyond the stage of a cellular strand, whereas in *Hynobius*, *Megalobatrachus* and *Menopoma* it becomes cartilaginous throughout its whole length. The anterior part of the pterygoid process disappears in the later larval stages of all these Urodeles. The continuity of the pterygoid process with the outer posterior part of the nasal capsule in *Ranodon* is of later

development, during adult life, and is not due to a persistence of an original connection with the antorbital process.

The pterygoid process ends free in *Triton*, *Salamandra*, *Plethodon*, *Amphiuma* and *Siren*. It is not developed in *Necturus*.

These phenomena indicate an ancestral Urodelan condition in which the pterygoid process was continuous anteriorly with the Trabecula, i.e. one in which there was a Pterygo-quadrate.

Gaupp held that the Commissura quadrato-cranialis anterior of the larval stage of *Rana* has no "analogue" in Urodela, but the new information above mentioned shows that it is homologous with the pterygoid process of Urodela, and should be similarly named[1]. The later-developed "pterygoid process" of Gaupp might have a new name.

In a 35 mm. larva of *Ichthyophis* the anterior end of the pterygoid process is in contact with the Trabecula. The only available larva of *Siphonops* was too far advanced in development for this—if present in younger stages—to be seen.

In *Ceratodus* there is no pterygoid process, or but (according to Greil) a transitory rudiment of one. In *Lepidosiren*, according to Agar, it is represented by a strand of dense connective tissue passing to a palatine tooth.

(2) The ascending process of the Quadrate is not present in *Lepidosiren* and *Protopterus* (Agar). It is present in *Ceratodus*, the larval stage of Urodela and Anura, and *Ichthyophis*, and is fused with either the trabecular wall or Taenia marginata. In *Siphonops* larvae, of which only a late stage was available, there is a joint. The cartilaginous continuity persists except in adult Gymnophiona, in which there is a fibrous union.

(3) The site of the union of the Quadrate with the base of the Chondrocranium varies. In *Lepidosiren* and *Protopterus* the basal process of the Quadrate fuses with the Trabecula, in Ceratodus with the junction of the Trabecula and Parachordal. In *Menopoma* and *Megalobatrachus* the basal process grows from the base of the pterygoid process, and not from the body, of the Quadrate. In the former it fuses with the basal plate, in the latter with a lateral process of the basal plate. In Amblystoma it fuses with the basal plate In *Necturus* it fuses with the praefacial commissure. In other Urodela and in Anura it fuses with the inner part of the floor of the auditory capsule. A syndesmotic joint subsequently develops in the basal bridge in *Plethodon*, *Hynobius*, *Salamandrella* and *Ranodon*. In *Siphonops* and *Ichthyophis* a lateral process of the basal plate develops—similar to that of *Megalobatrachus*. This in *Siphonops* fuses with the base of the pterygoid process. A diarthrodal joint develops in it subsequently. In *Ichthyophis* the process, which has only a transitory existence, does not fuse with the Quadrate, but is tied to it by fibrous tissue.

Comparison of the above series of forms with *Acanthias*, *Notidanus* and *Lepidosteus* (*vide infra*) suggests that the original site of basal union is with the Trabecula. This is also present in *Lepidosiren* and *Protopterus*. The other situations are due to various degrees of backward displacement. *Menopoma*,

[1] I have done so in figs. 71–73.

Megalobatrachus, *Siren*, *Amblystoma* and Gymnophiona are, in this, more primitive than other Urodela or Anura.

Versluys was of opinion that the basal s. basipterygoid joint of Amphibia is a very old phylogenetic feature, and in support of this theory adduced the observations of Veit on *Lepidosteus*. Such an opinion, however, does not account for the fact that—as Veit stated, though not referred to by Versluys—the development of a basal joint in *Lepidosteus* is preceded by a complete fusion of the Quadrate with the Chondrocranium at this point. A similar fusion preceding the formation of a joint takes place in *Acanthias*, *Siphonops*, *Plethodon*, *Hynobius* and *Salamandrella*. The developmental phenomena in all these cases can be explained by the theory of descent from forms possessing a fixed Quadrate. The Secondary feature of a joint may have been independently acquired. Further, the varying sites of such a joint support the theory that its development occurred at various phylogenetic stages in the backward shifting of the basal connection of the Quadrate with the Chondrocranium and, so, independently.

The above phenomena come out most clearly in a tabular statement:

The basal process fuses with	Trabecula	Junction of Trabecula and Parachordal	Basal plate	Praefacial commissure	Floor of auditory capsule
Protopterus	+	.	.	.	.
Lepidosiren	+	.	.	.	.
Acanthias	+*	.	.	.	.
Notidanus	?+*	.	.	.	.
Lepidosteus	+*	.	.	.	.
Ceratodus	.	+	.	.	.
Menopoma	.	.	+	.	.
Megalobatrachus	.	.	+	.	.
Siren	.	.	+	.	.
Siphonops	.	.	+*	.	.
Ichthyophis	.	.	A joint	.	.
Necturus	.	.	.	+	.
Amblystoma	.	.	+	.	.
Triton	.	.	.	.	+
Salamandra	.	.	.	.	+
Desmognathus	.	.	.	.	+
Spelerpes	.	.	.	.	+
Plethodon	.	.	.	.	+*
Amphiuma	.	.	.	.	+
Hynobius	.	.	.	.	+
Salamandrella	.	.	.	.	+*
Ranodon	.	.	.	.	+*
Anura	.	.	.	.	+*

* Subsequently a joint.

(4) The otic process of the Quadrate fuses with the outer wall of the auditory capsule in *Ceratodus*, Urodela and Anura. In *Lepidosiren* and *Protopterus* it fuses with an anterior process of the outer wall of the auditory capsule. In *Ichthyophis*, according to Marcus, it is present as a transitory process which does not fuse with the auditory capsule. This was not present in my larvae of *Ichthyophis* or *Siphonops*.

The above phenomena are summarised in the following tabular statement.

Dipnoi	Monimostylic	Streptostylic
Ceratodus	+	.
Protopterus	+	.
Lepidosiren	+	.

Amphibia	Larva: Monimostylic	Larva: Semi-streptostylic	Adult: Monimostylic	Adult: Semi-streptostylic
Urodela*				
Amblystomidae. Amblystoma punctatum	+	.	+	.
Amblystomidae. Amblystoma tigrinum	+	.	+	.
Salamandridae. Triton cristatus	+	.	+	.
Salamandra atra	+	.	+	.
Plethodontidae. Desmognathus fuscus	+	.	+	.
Spelerpes bislineatus	+	.	+	.
Plethodon cinereus	.	.	Early adult +	Older adult +
Amphiumidae. Amphiuma tridactylum	+	.	+	.
Hynobidae. Hynobius nebulosus	Earlier +	Later +	.	+
Salamandrella Keyserlingii†	Earlier +	Later +	.	+
Ranodon sibiricus	+	.	.	+
Cryptobranchidae. Megalobatrachus maximus	+	.	+	.
Menopoma alleghaniense	+	.	+	.
Proteidae. Necturus maculatus	+	.	+	.
Sirenidae. Siren lacertina	+	.	.	.
Anura. Rana	+	.	.	+
Gymnophiona. Ichthyophis glutinosus	.	+	.	Streptostylic +
Siphonops braziliensis	.	+	.	+

* I follow the classification of Dunn.

† s. Hynobius Keyserlingii (Dunn).

It would appear from the above that *Amblystoma, Triton, Salamandra, Desmognathus, Spelerpes, Amphiuma, Megalobatrachus* and *Menopoma*, are monimostylic in both the larval and adult states, and that *Necturus* and *Siren* are also monimostylic. The semistreptostylic condition of *Plethodon, Hynobius, Salamandrella* and *Ranodon* is preceded by an earlier monimostylic one.

It is, further, observable that the distribution of a long pterygoid process continuous anteriorly with the Trabecula, and of a basal joint, is not identical. The former occurs among Amblystomidae, Hynobidae, and Cryptobranchidae, whereas a basal joint occurs among Plethodontidae and Hynobidae, and in the former group not as a familial but only as a generic feature. Thus a joint develops in *Plethodon* but not in *Desmognathus* or *Spelerpes*. These occurrences do not harmonise with the theory of Versluys and Luther that the joint is an old phylogenetic feature.

The phenomena indicate, I think, that Urodela are descended from a monimostylic stock.

A pterygoid process may fail to be developed, e.g. *Necturus*, or not reach the Trabecula, e.g. *Triton*, or subsequently separate from it, e.g. *Amblystoma, Menopoma*, without the occurrence of any other skeletal change. On the other hand, the development of a basal joint does not occur as an isolated feature in *Ranodon, Plethodon, Hynobius* and *Salamandrella*. The anterior part of the pterygoid process either atrophies or fails to be developed. In *Ranodon* the continuity of the pterygoid process with the nasal capsule is a subsequent event.

Anura are monimostylic in the larval, semi-streptostylic in the adult, state. In Gymnophiona no larva is known in which the Quadrate is fixed to the

Chondrocranium by four processes. In larvae of *Ichthyophis*, however, the ascending process is at one period continuous with the Taenia marginata, and the extremity of the pterygoid process in contact with the Trabecula, and there is a (subsequently atrophying) lateral process of the basal plate which is tied to the Quadrate by fibrous tissue. Peter also described an incomplete otic process. Further, in an advanced larva of *Siphonops* there is a cartilaginous continuity between the Quadrate and the lateral process of the basal plate. The Quadrate in Gymnophiona larvae may thus be continuous with the Chondrocranium at three points.

These phenomena suggest that the streptostylic condition of adult Gymnophiona is not primary, but secondary to an original monimostylic one. The contrary opinion fails to explain the above-described structures.

The skeletal evidence thus suggests that Amphibia, like Dipnoi, are descended from autostylic and monimostylic ancestors. Further, the resemblance between the connections of the Quadrate with the Chondrocranium in Dipnoi and Amphibia is so close that, unlike Luther, I think it improbable that they have been separately acquired. This probability is rendered greater by consideration of the masticatory muscles—*vide infra*.

It is not without interest in regard to these speculations to note that in *Stegocephalia* and in *Lysorophus*—a member of the ancestral Urodeles from the Pennsylvanian deposits—the Quadrate was fixed (Case, Williston, Stromer, Luther, Sollas) though whether this monimostylic condition was of chondrogenetic origin, as in the Amphibia described above, cannot of course be determined.

Development of the Masticatory Muscles

Elasmobranchs. Marshall (1881) described the mandibular head-cavity of *Scyllium*, in stages K–M, as consisting of a dorsal dilated portion continuous with a laterally compressed ventral portion extending down the whole length of the mandibular arch. The main branch of the vth nerve lies wedged in between the mandibular and hyoid head-cavities. By the middle of stage M the dorsal portion of the mandibular head-cavity has atrophied and disappeared. The walls of the ventral prolongation become converted into muscles.

v. Wijhe (1882) stated that in stage K of *Scyllium* the second somite is continuous with the lateral plate in the mandibular segment. The R. mandibular v. crosses the outer side of the position where the second somite is continuous with the lateral plate and then runs down on its anterior side. The second somite forms the superior oblique muscle whilst the lateral plate develops into the mandibular muscles.

Miss Platt (1891) stated that in 14 mm. embryos of *Acanthias vulgaris* there is a thickening of the inner wall of the base of the second somite—the primordium of "muscle E," and an out-pocketing of the dorsal end of the mandibular muscle plate, forming a rudimentary muscle which comes to occupy a position close to the inferior oblique muscle of the eye. She traced "muscle E" up to the 26 mm. stage.

Hoffmann (1896) stated that in *Acanthias vulgaris* the medial and antero-medial walls of the second somite thicken and proliferate cells which develop into mesenchyme. He did not describe any "muscle E." The Levator labi superioris develops from the upper part of the walls of the mandibular muscle-plate (Kieferbogenhöhle), whilst the ventral part develops into the Adductor mandibulae. No figures were given of this development of the mandibular muscle-plate.

Lamb (1901) confirmed the account given of *Acanthias* by Miss Platt. He stated, however, that by the 27 mm. stage there were only the very slightest remains both of "muscle E" and of the rudimentary muscle at the dorsal end of the mandibular muscle-plate (which he called "muscle F").

Dohrn (1904), confirmed by Neal (1909, 1914 and 1918), showed that muscle E persists and forms the mandibular component of the Rectus externus. He also stated that the Adductor mandibulae develops from the ventral part of the mandibular muscle-plate, but did not give any details.

Klinkhardt (1905) stated that in *Spinax* embryos, with head-lengths of 2·73 and 2·96 mm. the R. mandibularis v. runs down on the outer side of the mandibular cavity. Guthke, too, stated that in 11 mm. embryos of *Torpedo ocellata* the R. mandibularis v. lies close to the wall of the mandibular cavity.

No one of the above investigators made mention of the Constrictor i. dorsalis.

In a paper published in 1911 I stated that in *Scyllium canicula* the mandibular muscle-plate separates into three portions—from above downwards the Constrictor i. dorsalis, the Adductor mandibulae, and the lateral half of the Intermandibularis. The relations of the R. mandibularis v. to the mandibular muscle-plate and to the muscles developing from it were not described. To determine this further material was examined. In a 14 mm. embryo (figs. 1–5) the primordium of the Obliquus superior is continuous with the mandibular muscle-plate. Both consist of an epithelium enclosing a cavity which is continuous from the one structure to the other. The uppermost part of the mandibular muscle-plate is roundish in transverse section. ·05 mm. below the Gasserian ganglion it fairly suddenly broadens antero-posteriorly into a plate, and there is a little upward projection—a "shoulder"—·03 mm. high, from it, behind the R. mandibularis v. The mandibular muscle-plate extends to the mid-ventral line. The united Ri. maxillaris and mandibularis v., issuing from the Gasserian ganglion, pass down lateral to the mandibular muscle-plate for a short distance and then separate; the former passes downwards and forwards, whilst the latter passes down about midway between the anterior and posterior edges of the muscle-plate.

In a 17 mm. embryo (figs. 6, 7) the appearances are similar, except that the "shoulder" of the muscle-plate posterior to the R. mandibularis v. has grown upwards and measures ·06 mm. in height.

In a 20 mm. embryo (figs. 8–11) the primordia of the Obliquus superior and the mandibular muscle-plate have separated. The Obliquus superior is

now solid; from it has separated a little flattened vesicle—the rudiment of muscle E—which is in contact with the anterior end of the Rectus externus. The cavity in the mandibular muscle-plate has disappeared owing to approximation of the medial and lateral walls. The muscle-plate consists of an upper part which is posterior to the R. mandibularis v. and broadens as it is traced downwards, a broad part with the nerve lying about its middle and a narrower ventral part. All these are in continuity.

In an embryo of 23 mm. (fig. 12) muscle E has fused with the Rectus externus. The primordium of the Palato-quadrate and Meckel's cartilage has developed. The mandibular muscle-plate is still a continuous strip, though one in which the future muscles are distinguishable. These are, from above downwards, the Constrictor i. dorsalis, the Adductor mandibulae and the lateral half of the Intermandibularis. The R. mandibularis v. is anterior to the upper part and crosses the lower part of the Constrictor i. dorsalis, i.e. this muscle is only in part formed by the upgrowing "shoulder" behind the nerve.

In an embryo of 29 mm. (fig. 13) the muscle-plate is fully separated into the muscles it forms. The upper end of the Constrictor i. dorsalis has grown up to the auditory capsule.

In an embryo of 35 mm. (figs. 14–17) the anterior end of the Adductor mandibulae has extended forwards to the roof of the nasal capsule.

In an embryo of 53 mm. a horizontal septum has developed in the Adductor mandibulae. There is as yet no definite separation of a Praeorbitalis from the anterior part of the upper portion of the Adductor.

The primordium of the masticatory muscles of *Scyllium* thus at first lies medial to the R. mandibularis v., with its upper end close to the Gasserian ganglion and continuous with the Obliquus superior. After separation of the latter, the mandibular muscle-plate becomes separated into the Constrictor i. dorsalis, Adductor mandibulae, and lateral half of the Intermandibularis. The upper end of the Constrictor i. dorsalis grows upwards and backwards behind the R. mandibularis v. to the auditory capsule. This upward growth begins to develop before the muscle-plate is separated from the Obliquus superior.

In 20, 21 and 22 mm. embryos of *Acanthias vulgaris* (figs. 21–23) the conditions are similar to those of the 20 mm. embryo of *Scyllium*. The primordium of the Obliquus superior has separated from the mandibular muscle-plate, and muscle E—relatively larger than in *Scyllium*—is confluent with the Rectus externus. The dorsal upgrowing end of the mandibular muscle-plate is posterior to the R. mandibularis v.; as it is traced down it is seen to broaden and the nerve to lie external to it about midway between the anterior and posterior edges.

In the various stages of *Scyllium* examined and in these embryos of *Acanthias* no "muscle F" was seen. It appears probable that it is identical with the upgrowing projection of the mandibular muscle-plate behind the nerve.

The description of the early stages of *Spinax* and *Torpedo* by Klinkhardt and Guthke, taken in conjunction with the position of the Constrictor i. dorsalis relative to the R. mandibularis v. in the adult forms of those fishes, suggests that a similar development takes place in them.

Luther was of the opinion that the Praeorbitalis had primitively a cranial origin and resembled the Adductor mandibulae in function. Subsequently, with increasing size of the eye and antero-posterior extension of the mouth, the Praeorbitalis separated from the Adductor and gained a more ventral origin.

Comparison of the developmental phenomena in *Scyllium* and *Heterodontus* does not support this view. In *Scyllium*, the Praeorbitalis is due to a forward growth of the Adductor and does not rise above the level of the Palato-quadrate, and even in a 53 mm. embryo cannot be distinguished from the upper portion of the Adductor (i.e. the part above the inscriptio) except by its origin from the nasal capsule. In a 47 mm. embryo of *Heterodontus* (fig. 25) the Praeorbitalis takes origin from a lateral projection of the nasal capsule and passes backwards nearly horizontally to join the Adductor. Its adult position with nearly vertical fibres (*vide* Luther's description and figure) is thus secondary.

Teleostomi. I stated that in embryos of *Acipenser*, *Amia* and *Lepidosteus*, the mandibular muscle-plate separates into the Constrictor i. dorsalis, Adductor mandibulae and Intermandibularis, but did not describe its relations to the Gasserian ganglion and the R. mandibularis v. To determine this further material was examined.

In a 6·5 mm. embryo of *Amia* (fig. 26) the mandibular muscle-plate is a vertical plate of cells, extending from the Gasserian ganglion downwards, its lower part curves inwards, but does not reach the mid-ventral line. It is medial to the R. mandibularis v. Its upper end diverges a little backward and is partly behind the Gasserian ganglion. (This position also holds true for the younger 5·5 mm. embryo.) The ventral end of the muscle-plate is continuous with that of the hyoid muscle-plate.

In a 7·5 mm. embryo (fig. 27) the mandibular muscle-plate is partially separated into the Constrictor i. dorsalis, Adductor mandibulae, and Intermandibularis. Its upper end diverges backward and outwards relative to the Gasserian ganglion. Its lower end is separated from that of the hyoid muscle-plate.

In an 8·5 mm. embryo (fig. 28) the Palato-quadrate and Meckel's cartilage have begun to develop. The Constrictor i. dorsalis, Adductor mandibulae, and Intermandibularis are fully separated from one another. Similar developmental phenomena occur in *Acipenser* and *Lepidosteus*.

Gregory (1905) stated that in a 9·0 mm. embryo of *Ceratodus* the 2nd (mandibular) head cavity is continuous ventrally with the central cavity in the mandibular arch. The musculature of the mandibular arch separates from it in later stages of development. The relation of these structures to the Gasserian ganglion is not depicted in this stage, but Gregory's figure 21 of

the 10·9 mm. stage shows the mandibular muscles extending, median to the R. mandibularis v., up to the ganglion.

I stated (1911) that the primordium of the masticatory muscles does not separate into upper and lower portions as it does in *Scyllium*, but divides into two vertical strips—the Pterygoid and Temporal muscles (called in this paper Levator mandibulae anterior and Levator m. posterior).

Terminology used in this paper	*Dipnoi*
Levator mandibulae anterior	*Ceratodus* Pterygoideus. Jaquet, Edgeworth, 1911 Portio temporalis of the Adductor mandibulae. Luther, 1913 Pseudo-temporalis s. Adductor m. internus. Luther, 1914 Temporalis. Greil, 1913 *Protopterus* Pterygoideus. Jaquet Temporalis. Owen, Pinkus, Luther, 1913 Temporal muscle. Humphry Pseudo-temporalis s. Adductor m. internus. Luther, 1914 *Lepidosiren* Temporalis Hyrtl. Bridge, Luther, 1913 Pseudo-temporalis s. Adductor m. internus. Luther, 1914
Levator mandibulae posterior	*Ceratodus* Adductor mandibulae s. Digastricus. Jaquet Temporalis. Edgeworth, 1913 Portio lateralis of the Adductor mandibulae. Luther, 1914 Portio lateralis s. Adductor m. posterior. Luther, 1914 Masseter. Greil *Protopterus* Masseter. Humphry, Luther, 1913 Masseter s. part of Adductor m. externus. Luther, 1914 Muscle temporalis. Jaquet *Lepidosiren* Masseter Hyrtl, Bridge, Luther, 1913 Masseter s. part of Adductor m. externus. Luther, 1914
Levator mandibulae externus	*Protopterus* Retractor anguli oris and Buccinatorius. Humphry Muscle labialis superior. Jaquet Retractor anguli oris. Luther, 1913 Retractor anguli oris s. part of Adductor m. externus. Luther, 1914 *Lepidosiren* Retractor labiorum. Hyrtl Retractor anguli oris superficialis and profundus. Luther, 1913 Retractor anguli oris s. part of Adductor m. externus. Luther, 1914

Greil (1913) stated that in a 5·4 mm. embryo of *Ceratodus* (with three gill-clefts reaching the ectoderm) the upper end of the mesoblast of the mandibular arch is continuous with its fellow across the mid-ventral line, and with that of the hyoid arch above and below the 1st gill-cleft. It has a notch in its upper border, in which lies the G. maxillo-mandibulare v. and a slight projection from its anterior border—the "ciliary" mesoderm. On section it shows two cavities in its upper part—the 2nd and 3rd head-cavities. The walls of the 2nd develop into the Temporal muscle, and those of the 3rd into the Masseter muscle. There are rudiments of a praemandibular gill-cleft opposite the junction of the Temporal and Masseter muscles. These muscles are consequently prae-

mandibular and mandibular formations. The G. ophthalmicum v. belongs originally to the praemandibular, and the G. maxillo-mandibulare v. to the mandibular arch. The Processus pterygoideus is the cartilage of the praemandibular, and the Quadrate that of the mandibular arch. In a 10·9 mm. embryo there is an anterior projection from the upper end of the Temporalis, which separates and forms the Obliquus superior. The notch in the upper end of the mesoblast deepens into a groove on its external surface. The N. maxillo-mandibularis v. runs in this groove, which deepens and separates the Temporalis from the Masseter. The primordia of the Temporalis and Masseter are continuous ventrally with that of the (lateral half of the) Intermandibularis until the stage of 11·6 mm. In an embryo of 13·9 mm. they are inserted into Meckel's cartilage. The Temporalis takes origin from the spheno-lateral cartilage and the cartilaginous bridge over the Incisura sphenotica, and the Masseter from the anterior surface of the Quadrate and its otic process. In an embryo of 17·8 mm. the origins of these muscles have spread to the antero-lateral surface of the auditory capsule.

Greil's theory that the Temporalis is a praemandibular, and the Masseter a mandibular, structure is open to many objections. (1) If, as Greil states, the G. ophthalmicum v. is a praemandibular, and the G. maxillo-mandibulare v. a mandibular structure, it might be expected that the Temporalis would be innervated by the former, and the Masseter by the latter. Now, both muscles (*vide* Luther) are innervated by the latter. (2) The Processus pterygoideus Quadrati is described by Greil as a small and transitory outgrowth from the Quadrate and not as an independent chondrification, as might be expected if, as he states, it is a praemandibular structure. I have however failed to find this pterygoid process in the embryos at my disposal. (3) The notch, deepening into an external groove for the N. maxillo-mandibularis v. separates an originally single undivided mass into two parts. Thus it is single in 6 and 9 mm. embryos (figs. 29–32), separated into two masses in a 11 mm. embryo (fig. 33). (4) If the outgrowth from the endoderm interpreted as the rudiment of a praemandibular gill-cleft is really such it should at least be constant in existence and position. Now, Greil represents it as a slight bulge of the endoderm opposite the anterior edge of the mesoderm mass in a 9·8 mm. embryo (fig. 278), and opposite the middle of the mesoderm mass in a 10·2 mm. embryo (fig. 287). Further, I have not been able to find any lateral bulge of the endoderm in front of the 1st gill-cleft in embryos of respectively 6 mm. (figs. 29 and 30), 7 mm., 8 mm., 9 mm. (figs. 31 and 32), and 11 mm. (fig. 33) in length. (5) If the theory were true it should be applicable to corresponding structures in Amphibia. But I have failed, in larvae of Urodela and *Rana*, to find any trace of what might be interpreted as a praemandibular gill-cleft, or of coalescence of two mesoderm masses into the primordium of the masticatory muscles, or of evidence of formation of the pterygoid process of the Quadrate from a separate centre.

These reasons, I think, justify rejection of Greil's theory, and it may be

stated that the primordium of the masticatory muscles separates into a part in front of the N. mandibularis v.—the Levator mandibulae anterior, and a part behind the nerve—the Levator mandibulae posterior. His "ciliary mesoderm" becomes the praemandibular somite—homologous with the similarly named structure in other Vertebrates.

This praemandibular segment was stated by Greil to give rise to the Recti superior and externus by two dorsal processes, and to the Rectus inferior and Obliquus inferior by a ventral process. The Obliquus superior was said to be derived from an anterior projection of the Temporalis (i.e. my Levator mandibulae anterior), which grows out in a 10·9 mm. embryo. In the figures it is represented as continuous with the Temporalis in embryos up to a length of 13·9 mm.

I find, however, that the external ocular muscles are developed somewhat differently. In an 11 mm. embryo (figs. 34–36) the praemandibular somite is an epithelium lined cavity internal to the under half of the eye, i.e. behind the ii. nerve, with a concave external wall next the eye and a convex medial wall, and horns projecting above and below the eye. The Recti superior, internus and externus, are present as primordia—thickenings of the convex medial wall of the cavity, the Rectus superior of the upper horn, the Rectus externus of the junction of the floor and the posterior wall. The Obliquus superior is proliferated from, but still continuous with, the upper wall of the dorsal horn. From this point it projects forwards and inwards.

In a 12 mm. embryo (fig. 37) the Obliquus inferior is proliferated from the ventral horn.

In a 12·5 mm. embryo all the muscles are quite distinct and formed. Figs. 38 and 39 show their appearance as seen from above and below. The Rectus internus is the muscle called Rectus inferior by Greil. I hold it to be an Internus as it passes from the trabecular wall outwards and forwards below the ii. nerve to the Bulbus oculi, to which it is attached below the Obliquus inferior. It is opposite the Rectus externus and not opposite the Rectus superior.

I cannot find any evidence that the Obliquus superior is formed from an anterior projection of the Temporalis muscle as is stated by Greil to be the case in embryos from 10·9–13·9 mm. in length. Thus, in the 11 mm. embryo I have depicted there is a gap of ·08 mm. between the Obliquus superior and the anterior surface of the Levator mandibulae anterior, and, as stated above, the Obliquus superior at this stage is still continuous with the wall of the praemandibular somite.

All the ocular muscles are thus formed from the convex medial wall of the praemandibular somite—the Recti superior, internus, and externus, from thickenings of the wall, the two Obliqui from cells proliferated from it.

In Protopterus and Lepidosiren there are, a Levator mandibulae anterior, Levator mandibulae posterior, and Levator mandibulae externus, the last mentioned being represented in Protopterus by the Retractor anguli oris and

in *Lepidosiren* by two muscles—the Retractor anguli oris superficialis and profundus. The development is not yet known for Agar's investigation did not extend to that of the individual muscles derived from the mandibular muscle plate. He stated that in stage 30 the future eye muscles are represented by a dense concentration of heavily yolked mesenchyme round the optic vesicle, which is continued by a narrow strand to the rudiment of the temporal muscle and can be traced further back curving in somewhat towards the middle line. There was no connection between this and the concentration of mesenchyme in the hyoid arch. No mention was made of a separate outgrowth from the dorsal end of the temporal muscle to form an Obliquus superior.

It would thus appear that in Dipnoi all the external ocular muscles are formed from the premandibular somite—an unexpected support of the theory I advanced in 1911 (*vide supra*, p. 226).

Luther was of opinion that the masticatory muscles of Dipnoi are collectively the homologue of the Adductor mandibulae of Selachii and Teleostomi. The above-cited observations of Gregory and Greil, however, show that the primordium of the masticatory muscles of *Ceratodus* has precisely the same relations to the R. mandibularis v. and the Gasserian ganglion as has the primordium of the Constrictor i. dorsalis l. Adductor mandibulae in *Scyllium* and *Amia*, i.e. it lies median to the nerve with its upper end close to the ganglion. Nor did these observers describe or depict the separation of any, subsequently atrophying, portion from the upper end of the primordium. I have, too, failed to discover it in embryos from the length of 6 mm. upwards.

It follows that the masticatory muscles of *Ceratodus*, and so probably of *Protopterus* and *Lepidosiren*, are collectively the homologue of the Constrictor i. dorsalis+Adductor mandibulae of *Scyllium* and *Amia*, and not solely of the Adductor.

Another terminology is therefore adopted, corresponding to the primitive position of the muscles relative to the R. mandibularis v.—Levatores mandibulae anterior and posterior.

Luther pointed out the homology in all three animals of the muscle here termed Levator m. anterior, but his opinion in regard to the other masticatory muscles differs from that adopted here. He thought that whilst in *Ceratodus* there is an Adductor m. posterior (here called Levator m. posterior), on the other hand in *Protopterus* and *Lepidosiren* there is no Adductor m. posterior but only an Adductor m. externus.

Comparison, however, of the developmental stages of *Ceratodus* with the figures given by Luther would make it probable that whereas in *Ceratodus* the Levator m. posterior lies in early stages posterior to the R. mandibularis v. and subsequently hypertrophies and bulges forward lateral to the nerve (cf. figs. 33 and 40); on the other hand, in *Protopterus* and *Lepidosiren*, the Levator m. posterior retains its primitive position posterior to the nerve.

Luther was of opinion that the Retractor anguli oris of *Protopterus* (and its homologues in *Lepidosiren*) is a part of (his) Adductor m. externus. He

subsequently pointed out its homology with (his) Adductor m. externus of Urodela. Now the latter muscle (which I call Levator m. externus) is developed from the Levator m. anterior (*vide infra*), so that it is possible that a similar development will be found to occur in these Dipnoi.

No definite opinion, however, in regard to these matters is possible until the development is known.

Urodela. Luther[1] distinguished the following muscles, which he classified according to their relationship to the branches of the vth nerve.

Named employed in this paper	*Luther's names*
Levator bulbi	Levator bulbi
Levator m. anterior (anterior to V_3)	Adductor m. anterior (rostral or medial to V_2 and V_3)
Levator m. posterior (medial or caudal)	Adductor m. posterior (caudal to V_3)
Levator m. externus (lateral to V_3)	Adductor m. externus (lateral to V_2 and V_3)

The Adductor m. anterior was further subdivided by Luther into the Pseudotemporalis and Pterygoideus.

Scott and Osborn (1879) stated that in Triton the section of the pleuroperitoneal cavity in front of the first gill-cleft becomes separated into two portions, each of which is lined by a columnar epithelium. The anterior portion lies close to the optic vesicle, whilst the posterior is enclosed entirely in the mandibular arch. The subsequent development was not followed.

Miss Platt (1897) stated that in 11 mm. embryo of *Necturus* (the first stage described) the mesothelial tissue of the mandibular arch is dorsally separate from that of the hyoid arch and passes directly into mesenchyme; ventrally it unites with that of the hyoid arch. The upper part divides into an external portion, the masseter (= A.m. externus, of Luther), and an internal portion, the temporalis (= A.m. internus posterior, of Luther), whilst the ventral part becomes the mylohyoid. The relations of these structures to the Gasserian ganglion and to V_3 were not described, nor was the development of the ocular muscles followed.

In a 15 mm. larva of *Menopoma* (figs. 53–55) the primordium of the masticatory and Intermandibularis muscles is a dorso-ventral strip of cells in front of the 1st gill-cleft. Its upper end is lateral to the Gasserian ganglion. It passes down internal to the R. mandibularis v. Its ventral end is continuous with that of the hyoid muscle-plate. The anterior edge of the upper part of the muscle-plate is continuous with the premandibular somite[2]. The cells of the latter are crowded with yolk-granules.

[1] Luther gave a complete list of the names employed by previous writers, which it is not necessary to quote.

[2] The development of the ocular muscles could not be followed owing to defective fixation of the younger larvae. I hope to do this later.

In a larva of 16 mm. (figs. 56–58) the muscle-plate has separated into the masticatory muscle-plate and the Intermandibularis. The premandibular somite has separated from the former. The relations of the muscle-plate to the R. mandibularis v are as in the previous stage.

In a larva of 20 mm. (figs. 59–61) the primordium of the masticatory muscles still forms a continuous whole. Its dorsal end extends up to the Crista trabeculae. The Levator bulbi is formed as an outgrowth from the anterior surface of the primordium—i.e. from the part which forms the Levator mandibulae anterior—at the level of the inferior border of the eye and slightly below the middle of the primordium. The outgrowth is ·03 mm. thick, it is ·36 mm. below the upper end and ·26 mm. above the lower end of the primordium. From the lower part of the primordium there is a backward outgrowth external to the R. mandibularis v. This is the Levator mandibulae externus. It extends upwards towards the otic process of the Quadrate which is beginning to form.

In a larva of 24 mm. (fig. 62) the Levatores m. anterior, posterior, and externus have separated from one another. The Levator m. anterior takes origin from the Crista trabeculae, the Levator m. posterior from the Quadrate, and the Levator m. externus from the otic process. The Levator bulbi has separated from the Levator m. anterior and forms a thin plate of cells below the eye.

In a larva of 28 mm. (fig. 63) the Levator bulbi has extended outwards, and also inwards towards the Trabecula.

There is a similar development of the Levator bulbi as an outgrowth of the anterior surface of the Levator m. anterior, in 16 mm. larvae of *Hynobius* and in 23 mm. larvae of *Triton cristatus*.

Anura. Luther distinguished the following muscles, which he classified according to their relationship to the R. mandibularis.

Names employed in this paper	*Luther's names*
Levator bulbi	Levator bulbi
Levator mandibulae anterior (anterior to V_3)	Pterygoideus s. Adductor m. internus (medial to V_2 and V_3)
Primordium of: Levator mandibulae externus (lateral to V_3)	Adductor m. externus (lateral to V_3)
Primordium of: Levator mandibulae anterior subexternus	Adductor m. posterior subexternus
Primordium of: Levator mandibulae anterior lateralis	Adductor m. posterior lateralis
Primordium of: Levator mandibulae anterior articularis	Adductor m. posterior articularis
Levator mandibulae posterior (superficialis and profundus) (posterior to V_3)	Adductor m. posterior (superficialis and profundus)

Luther stated that in a 7-day *Bombinator* larva (? length) the precartilaginous Palato-quadrate is at right angles to the long axis of the body, with a Proc. muscularis, a Proc. ascendens, and a Commissura quadrato-cranialis anterior. The originally undivided primordium of the masticatory muscles has separated into a more superficial portion caudal to V_3—the Adductor mandibulae posterior, and an inner layer medial to V_3—medial to V_3 the Pterygoideus. The outer layer is a continuous one, being marked only by the different origins

of the fibres—from the Pars metapterygoidea the Adductor posterior longus profundus and superficialis, and from the Processus muscularis the Adductor posterior subexternus, lateralis, and articularis. These muscle-primordia have, as already pointed out by Goette, an almost vertical position which closely resembles that of the adult. A rotation subsequently occurs so that they lie almost horizontally with the original upper ends posterior and the original lower ends anterior.

In an 8 mm. larva of *Rana temp.* (figs. 67, 68) the mandibular muscle-plate is in a vertical position, at right angles to the longitudinal axis of the body. Its upper end is medial to the lower end of the Gasserian ganglion. The R. mandibularis passes down lateral to the muscle-plate for a little distance.

In a 9 mm. larva (figs. 69, 70) the muscle-plate has separated into dorsal and ventral portions, the masticatory muscle-plate and the Intermandibularis. The upper end of the former is close to the Gasserian ganglion, as in the previous stage. It passes downwards and forwards below the eye, at about 45° to the longitudinal axis of the body. It is partially separated into the Levator mandibulae anterior and Levator m. posterior.

In a 9·5 mm. larva (figs. 71–75) the masticatory muscle-plate is nearly in a horizontal position so that what was anterior is now dorsal, and what was posterior is now ventral. It is fully separated into Levator m. anterior and Levator m. posterior. As these muscles are traced forwards it is seen that they have a mutual twist, so that in front the Levator m. anterior is below ("morphologically" posterior to) the Levator m. posterior. The R. mandibularis v. passes over the Levator m. posterior, obliquely forwards and downwards. The posterior ("morphologically" dorsal) part of the Levator m. posterior is partially separated into the Levator m. posterior superficialis and Levator m. p. profundus. Two outgrowths are given off from the lateral side of the front end of the Levator m. anterior—the primordium of the Levatores m. anterior subexternus, articularis, and lateralis below ("morphologically" posterior to) the R. mandibularis v. and the Levator m. externus above ("morphologically" anterior to) the nerve. These outgrowths occur from the lower part of the Levator m. anterior which is overlapped by the Levator m. posterior.

In a larva of 10 mm. (fig. 76) these outgrowths have separated. The primordium of the Levator bulbi is in process of being proliferated from the upper ("morphologically" anterior) surface of the Levator m. anterior. It extends over ·04 mm. and is situated under the eye, rather above the middle of the Levator m. anterior—this muscle extending ·2 mm. behind and ·33 mm. in front of the primordium.

In a larva of 11 mm. (fig. 77) the primordium of the Levator bulbi is separated from the Levator m. anterior. It can be seen in succeeding stages up to one of 20 mm. (fig. 78) in much the same condition. In a larva of 21 mm. (fig. 79) in which the hind legs are just visible externally, the Levator bulbi

has greatly developed and spread, dorso-internally towards the side wall of the Chondrocranium, and externally under the eye.

As stated above, Goette and Luther showed that in *Bombinator* larvae the primordium of the masticatory muscles begins to separate into muscles before the forward movement of its lower end occurs. I find that in a larva of 8 mm. (figs. 80–83) the primordium is situated vertically and has separated into Levator m. anterior and Levator m. posterior, and the latter is beginning to divide into its superficialis and profundus portions. The dorsal end of the Levator m. anterior is anterior, and that of the Levator m. posterior is posterior, to the R. mandibularis v. As the muscles are traced down it is seen that they mutually twist round one another, so that ventrally the Levator m. anterior is posterior to the Levator m. posterior. In a larva of 9 mm. the shifting forwards of the lower ends of these muscles has taken place and the condition approximates to that of *Rana*.

Gymnophiona. Luther distinguished the following muscles:

Names employed in this paper	*Luther's names*
Compressor glandulae orbitalis	Compressor glandulae orbitalis
Levator mandibulae anterior	Pseudotemporalis Adductor externus
Levator quadrati	Levator quadrati
Levator mandibulae externus	Adductor m. externus minor
Levator mandibulae posterior	Pterygoideus

Marcus (1909 and 1910) stated that the primordium of the mandibular muscles in stages 20 and 24 of *Hypogeophis* is continuous dorsally with the 2nd or mandibular somite. Its upper end, in these stages, lies immediately beneath the G. maxillo-mandibulare v. In stage 28 the mandibular somite has separated from the primordium of the masticatory muscles. The former was said to develop into the Rectus superior, Rectus inferior, Obliquus inferior and perhaps the Rectus internus. The development of the primordium of the masticatory muscles was not followed.

The Obliquus superior was said to develop from the lateral plate of the premandibular somite. The 3rd somite was said to develop into the Rectus externus, Retractor tentaculi and perhaps the Rectus internus.

The development of the Compressor glandulae orbitalis was not followed.

Norris and Hughes (1913) stated that the Compressor glandulae orbitalis is innervated by a branch of the R. mandibularis v. in *Dermophis, Herpele* and *Geotrypetes*[1].

In a 28·5 mm. larva of *Ichthyophis*—the youngest available—(figs. 92–94) the primordia of the masticatory muscles consist of aggregates of round and spindle-shaped cells. There are as yet no muscle fibres. The R. mandibularis v. passes outwards above the pterygoid process of the Quadrate, and then downwards outside Meckel's cartilage. In front of this nerve is the Levator m.

[1] They further add that the statement of Marcus that this muscle is innervated by the iii. is obviously an error. I cannot find, however, that Marcus did make this statement.

anterior, behind it the Levator m. posterior. The Levator m. anterior is a triangular mass, the upper edge of which is just outside the Taenia marginata and, posteriorly, just beneath the upper part of the ascending process of the Quadrate. The posterior edge is vertical. The apex is close to Meckel's cartilage. The primordium of the Levator quadrati is present on the inner surface of the Levator m. anterior, from which it is not quite separated. It slopes downwards and backwards towards the pterygoid process of the Quadrate. The Levator m. posterior passes downwards from the ascending process towards Meckel's cartilage. It is far less in size than the Levator m. anterior.

In a larva of stage 2 (figs. 95–97) (a larva of which the tail was broken off and the length of which could not be determined but which in development was intermediate between the 28·5 and the 35 mm. larvae) the primordium of the Compressor glandulae orbitalis has developed. It is a column of cells which is posteriorly continuous with the anterior surface of the Levator m. anterior, and projects forwards for a little distance. The Levator quadrati is fully separated from the inner surface of the Levator m. anterior. The posterior end of the Levator m. anterior projects backwards external to the R. mandibularis v. and the Levator m. posterior. This is the primordium of the Levator m. externus. The Levator m. posterior has an additional head from the pterygoid process of the Quadrate and the pterygoid bone.

In a 35 mm. embryo (figs. 98, 99) the Levator quadrati has an additional insertion into the pterygoid bone. The Levator m. posterior is partially separated into two, corresponding to its primary and secondary heads of origin; the latter fibres pass downwards and backwards.

In a 59 mm. embryo (fig. 103) the Compressor glandulae orbitalis has separated from the Levator m. anterior. The upper end of the latter has spread backwards over the parietal bone. The Levator m. externus is a separate muscle. The lower, secondary, head of the Levator m. posterior, arising from the pterygoid process and the Pterygoid bone, passes backwards on the medial side of the jaw towards the extremity of the retroarticular process.

In the adult stage (*vide* Luther), the primary head of the Levator m. posterior from the ascending process has disappeared.

The masticatory muscles of a 70 mm. larva of *Siphonops* (figs. 84–89) resemble those of the 59 mm. larva of *Ichthyopis*, with the following exceptions. (1) The Levator m. anterior has no origin from the ascending process of the Quadrate. (2) The primary head of the Levator m. posterior from the ascending process of the Quadrate—presumably present in earlier stages—has disappeared, and only the secondary head of the muscle exists—taking origin from the pterygoid process of the Quadrate, the basipterygoid process and the os basale.

Discussion. Luther was of the opinion that the Levator bulbi of Urodela and Anura, and the Levator quadrati and Compressor glandulae orbitalis of Gymnophiona, are the homologues of the Constrictor i. dorsalis of Elasmobranchs and Teleostomi; whilst the jaw muscles of Amphibia are (collectively) the homologue of the Adductor mandibulae of these fishes.

Now, in *Menopoma, Hynobius, Triton cristatus,* and *Rana temp.* the Levator bulbi is formed from cells proliferated from the anterior surface of the Levator anterior, whilst in just earlier stages no trace of these cells is visible. On Luther's theory it should have been possible to detect a primordium becoming detached from the dorsal end of the primordium of the masticatory muscles and moving down to the position it occupies. This was not found. Further, if Luther's theory were true it should be found that the Levator quadrati and Compressor glandulae orbitalis of *Ichthyophis* are developed from a common primordium of the masticatory muscles and then separating into two—one passing to a position internal to the Levator anterior to form the Levator quadrati, and the other to a position in front of it to form the Compressor glandulae orbitalis. This was not found. The Levator quadrati is separated from the internal surface of the Levator anterior and the Compressor glandulae orbitalis is proliferated from its anterior surface. It is concluded that Luther's theory is not tenable.

Further, it is observable that the primordium of the masticatory muscles in *Menopoma, Hynobius, Rana,* and *Ichthyophis* extends from the Gasserian ganglion to the jaw just as does that of the Constrictor i. dorsalis + Adductor mandibulae in *Scyllium* and *Amia.*

The primordium of the masticatory muscles of these Amphibia is thus homologous with that of the Constrictor i. dorsalis + Adductor mandibulae, and not solely with the latter. The terms Levatores mandibulae are consequently employed instead of Adductores mandibulae. In this respect Amphibia are very like *Ceratodus.* The resemblance between the primordium of the masticatory muscles of Amphibia and *Ceratodus* extends to the muscles into which it develops. In Dipnoi the masticatory muscles can be classified according to their relationship to the R. mandibularis v. into Levatores m. anterior, posterior, and externus. The same thing is true of Amphibia—as was also pointed out by Luther. The developmental phenomena, however, suggest some modification of his opinions.

In early stages of *Menopoma* the primordium of the masticatory muscles is median to the R. mandibularis v., extending in front of and below the nerve. It separates into Levatores m. anterior and posterior. The Levator m. externus is formed by outward and backward growth from the Levator m. anterior external to the nerve. The Levator bulbi is proliferated from the anterior surface of the Levator m. anterior.

Determination of the homologies of the masticatory muscles of *Rana* with those of Urodela is rendered a little difficult by three facts: (1) Their primordium begins to separate into individual muscles during the forward movement of the lower end. (2) The lower parts of the Levator m. anterior and Levator m. posterior twist round one another so that the ventral end of the Levator m. anterior is below ("morphologically" posterior to) that of the Levator m. posterior. (3) The R. mandibularis v. crosses over the Levator m. posterior obliquely forwards and downwards.

In the larva of *Bombinator*, however, the primordium of the masticatory muscles separates into the Levator m. anterior and Levator m. posterior whilst the primordium is still in a vertical position, so that determination of their morphological value becomes possible. It is seen that the lower ends of the Levators twist round one another. The insertion of the Levator m. anterior, posterior to that of the Levator m. posterior, is thus not related to the secondary horizontal position of the muscles in the larva. It persists in the adult stage of Anura (*vide* the description and figure of Luther).

The Levator m. externus of *Rana* is proliferated from the lateral surface of the Levator m. anterior and grows backwards and outwards above (i.e. "morphologically" anterior to) the R. mandibular v. exactly as in *Menopoma*. The primordium of the Levatores m. subexternus, lateralis, and articularis is proliferated from the lateral surface of the Levator m. anterior below (i.e. "morphologically" posterior to) the R. mandibularis v.

Owing to the mutual twist of the lower ends of the Levatores m. anterior and posterior, the Levator m. externus and the primordium of the Levatores m. subexternus, lateralis, and articularis are proliferated from the Levator m. anterior below ("morphologically" posterior to) the Levator m. posterior.

These developmental phenomena show that the Levatores subexternus, lateralis, and articularis cannot be regarded as portions of the Levator m. posterior—as was thought by Luther (his terms being, of course, "Adductores").

The Levator bulbi is proliferated from the anterior surface of the Levator m. anterior, as in *Menopoma*, *Hynobius* and *Triton*.

As regards Gymnophiona, the muscle here called Levator m. anterior corresponds to Luther's Pseudo-temporalis + Adductor m. externus. He stated that his Adductor m. externus is homologous with the similarly named muscle of Urodela and Anura. But it is difficult to believe this, for—as he himself states—it lies anterior and not external to the R. mandibular v. Further, in transverse sections of these larvae of *Ichthyophis* and *Siphonops* I failed to find any separation of the muscle-mass in front of the R. mandibular v. into two portions. The Ri. maxillaris v. and buccalis pierce it from behind forwards, but the muscle-fibres are in apposition above and below those nerves. There is thus only one muscle, the Levator m. anterior, and the separation into medial and lateral parts described by Luther and by Norris and Hughes is of late development.

The Levator quadrati is separated from the inner surface of the Levator m. anterior. It is not formed dorsal to the Levator m. anterior and subsequently move down to its permanent position—as would be the case if it were homologous with the Constrictor i. dorsalis of Selachii and Teleostomi. It has no homologue in Urodela, not even in those Urodela which become semi-streptostylic.

The Compressor glandulae orbitalis is proliferated from the anterior surface of the Levator m. anterior, just as is the Levator bulbi of Anura and

Urodela. It has no genetic association with the Levator quadrati, as Luther supposed. The recent determination of its innervation by Norris and Hughes from the R. mandibularis v. in *Dermophis*, *Herpele*, and *Caecilia*, agrees with this.

Luther stated that there is no Adductor m. posterior in Gymnophiona, and that the "Pterygoideus" is homologous with the similarly named muscle of Urodela. Now the Pterygoideus of Urodela is one of the subdivisions of the Levator m. anterior, whilst the "Pterygoideus" of Gymnophiona is the Levator m. posterior, which acquires a secondary origin from the Pterygoid process and Pterygoid bone, whilst its insertion extends back to the end of the retroarticular process. I therefore regard the "Pterygoideus" of Luther as homologous with the Levator m. posterior of Urodela and Anura.

The muscle here termed Levator externus is identical with the Adductor externus minor of Luther. He stated that it is probably part of his Adductor externus, the separation being due to the passage of a couple of sensory nerves between the two portions. He added that it might be homologous, perhaps only analogous, with the Adductor posterior lateralis of Anura. I find that it is an outgrowth from the Levator anterior, lateral to the R. mandibularis v., just as in *Menopoma* and *Rana*, and consequently regard it as a Levator externus.

The above can be summed up in the following table:

	Levator mandibulae anterior				Levator mandibulae posterior
		Levator mandibulae externus	Levator bulbi or Compressor glandulae orbitalis	Levator quadrati	
Ceratodus	+	0	0	0	+
Protopterus	+	+	0	0	+
Lepidosiren	+	+	0	0	+
Urodela	+	+	+	0	+
Anura	+	+	+	0	+
Gymnophiona	+	+	+	+	+

Comparison of the masticatory muscles of Dipnoi and Amphibia brings out the following points:

The Levator m. anterior is large and simple in Dipnoi. It separates into the Pseudo-temporalis and Pterygoideus, of Luther, in Urodela. It gives off the primordium of the Levatores m. subexternus, lateralis, and articularis, in Anura. It separates into two parts at a late stage in Gymnophiona. This separation is not homologous with that which takes place in Urodela.

The Levator m. externus is absent in Ceratodus, and quite small in *Protopterus*, *Lepidosiren*, Anura and Gymnophiona. It is greatly developed in Urodela.

The Levator m. posterior is large in Dipnoi, especially in Ceratodus. It is much less developed in Urodela, Anura, and Gymnophiona. In the last-mentioned group the original head from the ascending process of the Quadrate is lost during development and a secondary one gained.

The Levator quadrati of *Ichthyophis* and *Siphonops* has no homologue in Dipnoi, Urodela or Anura. Its formation is related to the development of streptostylism. The development of semistreptostylism in some genera of Urodela is not associated with any change in the masticatory muscles[1] nor with the formation of a Levator quadrati—a fact which when taken into association with the scattered distribution of semistreptostylism in Urodela (*vide* table, p. 236) harmonises with the theory deduced from the skeletal evidence that the conditions of streptostylism in Gymnophiona and of semi-streptostylism in Anura and some Urodela have been separately acquired in these families of Amphibia from an ancestral condition of monimostylism.

The argument in the above pages may be summed up as follows. In Selachii and Teleostomi the primordium of the masticatory muscles separates into dorsal and ventral parts—the Constrictor i. dorsalis and Adductor mandibulae. In Dipnoi and Amphibia it does not so divide into dorsal and ventral parts, but separates into dorso-ventral strips. The monimostylism which the skeletal evidence suggests as the primary condition in Dipnoi and Amphibia is related to this non-division of the primordium of the masticatory muscles into dorsal and ventral parts. The Levator bulbi of Urodela and Anura and the Compressor glandulae orbitalis of Gymnophiona are homologous structures, developed from cells proliferated from the anterior surface of the Levator mandibulae anterior. In Gymnophiona the secondary development of streptostylism is associated with the separation of a fasciculus from the medial surface of the Levator mandibulae anterior to form a Levator quadrati.

On the supposition, which is supported by the above-recorded phenomena, that Dipnoi and Amphibia have sprung from a common autostylic, monimostylic, stock, it is of interest to make comparison of the various cranial cartilages and muscles to ascertain in which groups the more primitive features occur.

Dipnoi are more primitive than Amphibia in:

1. The site of attachment of the basal process of the Quadrate.
2. The presence of an Epihyale (in *Ceratodus*).
3. The absence of a Fenestra vestibuli.
4. The condition of the hyoid muscles—consisting as they do of a Levator hyoidei), Interhyoideus, and Opercularis s. Constrictor hyoideus[2]. On the other hand, in Amphibia there is no Opercularis, and the Levator hyoidei

[1] It should be noted, however, that Luther states that in the adult condition of *Hynobius* and *Salamandrella* (which are semi-streptostylic) some fibres of the Levator bulbi are inserted into the pterygoid process of the Quadrate. This is of late development, e.g. it is not present in a 37 mm. larva of *Hynobius* in which the basal joint had already developed.

[2] According to Ruge the Levator hyoidei (C2 hd) is present in *Protopterus* but has almost entirely disappeared in *Ceratodus*—only the few bundles passing to the Hyomandibulare (the cartilage I call "Interhyale") can be regarded as its remains. I find, however, that it is in the adult a well-marked muscle passing, partially medial to the outer limb of the Interhyale, from the under surface of the auditory capsule to the apex and posterior edge of the Keratohyale. I do not find any fibres passing to the Interhyale. The condition is thus similar to that present in a 27 mm. embryo.

gains, in part or wholly, an insertion into the hind end of the lower jaw, forming a Depressor mandibulae.

5. The condition of the Constrictores branchiales (only known however in Ceratodus).

6. The number of Transversii ventrales.

7. The presence of a 5th branchial bar and musculature.

8. The condition of the laryngeal muscles.

Amphibia are more primitive than Dipnoi in:

1. The presence in some of a well-marked pterygoid process of the Quadrate, joining the Trabecula.

2. The number of the Subarcuales recti.

3. The absence of any backward extension of the hind end of the Genio-hyoideus (so that a Genio-coracoideus or Genio-thoracius is not formed).

4. The situation of the larynx, i.e. does not shift backwards.

5. The absence of a Constrictor oesophagi et laryngis.

Two features (1) the absence of a Levator mandibulae externus in Ceratodus, and (2) the absence of an ascending process of the Quadrate in *Lepidosiren* and *Protopterus*—are of doubtful phylogenetic significance. The first mentioned may perhaps be primary.

On the Relationship of the Quadrate and Masticatory Muscle of Elasmobranchii and Teleostomi with those of Dipnoi and Amphibia.

Swinnerton (1902), from his observations on the development of the skull of *Gasterosteus* and other Teleostomi, suggested that Elasmobranchii and Teleostomi sprang from a common ancestral stock with a Quadrate "bearing dorsally two, possibly three, processes; an anterior one, parallel with its fellow, and not united with it, but with the ethmoid plate, so that a moveable upper jaw did not exist; a middle one articulating with the trabecula, in the region lying between the optic and trigeminal nerves; a posterior one articulating with the auditory capsule." He did not take the masticatory muscles into consideration, nor did he make any reference to Dipnoi or Amphibia.

In 1911 I suggested a similar theory based on comparison of the development of the masticatory muscles in Elasmobranchii, Teleostomi, Dipnoi, and Amphibia. It differed from Swinnerton's in that the middle and posterior connections were supposed to be continuous, so that the Palato-quadrate was fixed to the Chondrocranium at three points. I now restate the theory, with additions due to later work.

Scyllium is hyostylic. In a 23 mm. embryo (fig. 12) the Trabeculae are not yet developed, and the (continuous) primordium of the Palato-quadrate and Meckel's cartilage is not connected with any other structure. In a 29 mm. embryo (fig. 13) the Palato-quadrate is chondrified; the primordium of the spiracular cartilage is formed as a procartilaginous upgrowth of the hind end

of the Palato-quadrate[1]. In a 35 mm. embryo (figs. 14–17) the antorbital process of the chondrocranium is formed; its antero-internal end is continuous with the Trabecula, and the roof of the nasal capsule. From this point it extends postero-externally. Its posterior end is continuous with the Palato-quadrate. The nasal roof itself has no relations with the Palato-quadrate, which at this stage does not extend so far forwards. The primordium of the spiracular cartilage is separated from the Palato-quadrate. In a 53 mm. embryo (figs. 18–20), in which the cartilages are more fully chondrified, the posterior end of the antorbital process has extended further backwards. Its antero-internal end is still continuous with the Trabecula and the roof of the nasal capsule. A ligament passes from the back of the nasal roof to the dorsal surface of the Palato-quadrate, and another from the lateral edge of the antorbital cartilage to the Palato-quadrate. The spiracular cartilage is chondrified. The anterior end of the Palato-quadrate has extended further forward and meets its fellow.

There is thus in early stages a cartilaginous continuity between the Palato-quadrate and the antorbital process of the chondrocranium. This degenerates into a ligament.

Acanthias is streptostylic and amphistylic. The basal process of the Palato-quadrate articulates with the Trabecula. Sewertzoff showed that this basal joint is preceded by a continuity of the basal process with the Trabecula.

Notidanus (*Heptanchus*) is autostylic and streptostylic. Gegenbaur stated that the otic process articulates with the postorbital process of the cranium and that the basal process articulates with the cranium by a "Palato-Basal-gelenk." Huxley subsequently stated that the basal process is attached to the cranium by a strong ligamentous band. The basal connection is thus variable in character.

I find that in a 58 mm. embryo the basal joint with the Trabecula is already formed. The otic process of the Palato-quadrate and the post-orbital process of the chondrocranium are separated by a small gap filled with mesenchyme. In a 70 mm. embryo the postorbital joint has developed[2].

The postorbital joint is thus not preceded by any cartilaginous continuity. The basal joint may be so preceded, but earlier stages were not available.

Heterodontus (*Cestracion*) is amphistylic. Huxley stated that the huge Palato-quadrate is united to the skull in the praeorbital region by a joint, and in the orbital region by fibrous tissue. "An otic process, or spiracular cartilage, is connected to the periotic cartilage above and to the quadrate below the ligament."

[1] Six embryos of *Scyllium* of 29–30 mm. were cut before finding this. The other embryos were not old enough or too old to show the continuity of the primordium of the spiracular cartilage with the Palato-quadrate. The process of formation and budding off probably takes but a short time. These occurrences are merely an illustration of the fact that size is not an exact criterion of stage of development. They may explain the failure of Dohrn to find that the spiracular cartilage is formed from the Palato-quadrate.

[2] It is well seen in a model of this chondrocranium lately made by my colleague Dr Henderson.

I find that in a 47 mm. embryo (figs. 24, 25) the anterior end of the Palato-quadrate is in contact with the Trabecula. The primordium of the spiracular cartilage is a dorsal procartilaginous process of the hinder end of the Palato-quadrate. The upper end of the Hyomandibula articulates with the lower surface of the auditory capsule, and its lower end with the Palato-quadrate and Meckel's cartilage. The chondrocranium is very immature, and the Trabecula is nearly at right angles to the Parachordal. Older embryos were not available.

Ganoids. *Acipenser* is hyostylic. Parker stated that this condition is developed at a very early stage (8·5–9·5 mm. embryos) and that there is no connection with the chondrocranium. My observations confirm this.

Polyodon is hyostylic. The development is not yet known. Bridge stated that the Palato-quadrate has no connection with the cranium either directly or by ligament, but is suspended by its posterior extremity from the distal end of the Symplectic, to which it is attached by two slender ligaments.

Polypterus is hyostylic. Budgett stated that in a 30 mm. embryo the anterior end of the Palato-quadrate articulates with a facet on the ventral side of the nasal capsule.

Amia is amphistylic. The Pars palatina of the Quadrate articulates with the Planum ethmoidale, is tied to the Trabecula by a basipterygoid ligament and to the hinder wall of the orbit by a ligament. In a 19 mm. embryo (Swinnerton) the Palato-quadrate has a large basal process projecting towards the Trabecula, and the latter has a slight lateral process. The anterior end abuts against the Planum ethmoidale. I can confirm these statements.

Lepidosteus is amphistylic. In development (Parker, Veit) the anterior end of the Palato-quadrate is united to the Cornu trabeculare by cartilage (Parker), or firm connective tissue (Veit). Further back, the Palato-quadrate is united to the Trabecula by embryonic cartilage in which a basal joint subsequently develops (Veit). Later on, an otic process is developed and projects towards but does not reach the auditory capsule (Parker).

Teleostei. In *Gymnarchus* (Assheton) the Pars palatina of the Palato-quadrate is continuous with the Trabecula by precartilaginous tissue, and the Pars quadrata articulates with the auditory capsule (= an otic process). In *Gasterosteus* (Swinnerton) the Pars palatina articulates, and in some stages is continuous, with the side of the ethmoid plate. In many Teleostei, e.g. *Belone*, *Zoarcia*, *Salmo*, there is a basal process projecting from the Quadrate towards the Trabecula (Swinnerton). The mode of suspension is hyostylic only posteriorly, but autostylic anteriorly.

It would appear, therefore, that the Palato-quadrate is continuous with the Chondrocranium in some genera of Selachii and Teleostomi at two points—anteriorly and in the middle, corresponding to the anterior and basal continuities of Amphibia. Further, there is an otic process in *Heptanchus*, *Lepidosteus*, and *Gymnarchus*. In *Heptanchus* it articulates with the post-orbital process of the auditory capsule, in *Lepidosteus* it approaches but does

not touch, or articulate with, the auditory capsule, in *Gymnarchus* it articulates with it[1].

Dohrn stated that the spiracular cartilage is of independent formation in *Scyllium*, *Pristiurus*, *Mustelus*, *Raja*, and *Torpedo*. But in *Scyllium*, as shown above, it is formed as a procartilaginous outgrowth of the hind end of the Palato-quadrate and subsequently separates and chondrifies. Similarly, in *Heterodontus* it is formed as a procartilaginous outgrowth of the Palato-quadrate. This evidence shows that, as Huxley suggested, the spiracular cartilage is homologous with the otic process.

Gegenbaur was of opinion that the articulation of the otic process of *Heptanchus* with the post-orbital process represents the primary articulation with the Chondrocranium, whilst the basal connection is secondary. Huxley was of the reverse opinion. Luther held that the post-orbital connection is not an ancestral feature. It only occurs in certain groups, "in which the independently preformed processes came into connection with one another." This theory evidently does not offer any explanation of the otic process—a process which is of ancient origin, for Luther states that there are many fossil forms as far back as the oldest Selachians known in which there is an apposition ("Anlegen") or union of the Quadrate with the post-orbital process.

Comparison of the whole series of forms—Amphibia, Dipnoi, *Gymnarchus*, *Lepidosteus*, *Heptanchus*—suggests the existence of an ancestral continuity of the otic process with the outer surface of the auditory capsule, and that the joint with the post-orbital process of the last named is a secondary phenomenon. In development the post-orbital process is formed at a later stage than the auditory capsule.

The sum of these skeletal phenomena suggests that Selachii, Batoidei, and Teleostomi are descended from autostylic and monimostylic ancestors in which there was a Pterygo-quadrate united to the Chondrocranium at three points. The anterior end was probably fused with the ethmoid region. The middle region was probably fused to the Trabecula by a basal process. The otic process was probably fused with the auditory capsule. This condition was lost and a streptostylic one developed. *Heptanchus* is autostylic, the others amphistylic or hyostylic, whilst various traces are left in developmental phenomena or in adult anatomy of what existed in the past.

The development of a moveable Pterygo-quadrate was probably correlated with the formation of a Constrictor i. dorsalis, i.e. with a division of the primordium of the masticatory muscles into dorsal and ventral portions —the Constrictor i. dorsalis and Adductor mandibulae. The ontogenetic phenomena in *Scyllium* and *Amia* have been described above.

There are certain skeletal and muscle differences between these various groups. (1) In *Amia*, *Polypterus*, *Lepidosteus*, and Teleostei, the anterior process of the Quadrate, just as in Amphibia, does not extend further forwards than its connection with the Chondrocranium; whereas in the majority of

[1] Assheton did not state whether the articulation was preceded by a continuity of tissue.

Selachii, in Batoidei, *Acipenser*, and *Polyodon*, it is prolonged anteriorly, nearly or quite meeting its fellow. To mark this difference the former condition —probably the primary one—might be called a Pterygo-quadrate, the latter a Palato-quadrate. In successive developmental stages of *Acanthias*, *Scyllium*, and *Acipenser*, the anterior end of the bar can be seen extending forwards until finally it meets its fellow. (2) No Processus ascendens has been described in Selachii, Batoidei, and Teleostomi, whereas one is developed in *Ceratodus* and Amphibia. The latter condition is probably a later phylogenetic development. (3) In Selachii and Teleostomi the primordium of the masticatory muscles lies in early stages median to the R. mandibularis v. and shows no trace of division either then or subsequently into parts in front of and behind the nerve. On the other hand, in Dipnoi and Amphibia, the primordium of the masticatory muscles separates into parts in front of and behind the nerve, i.e. Levator m. anterior and Levator m. posterior. This division is probably a later phylogenetic development.

Holocephali are monimostylic, the Palato-quadrate fusing with the Chondrocranium during development (Schauinsland, Dean). There is no Constrictor i. dorsalis. The masticatory muscles were described by Vetter and by Luther in terms of an Adductor mandibulae. If it could be shown that a Constrictor i. dorsalis exists in early developmental stages and subsequently atrophies, this would confirm their opinion, and also be evidence that the monimostylic condition is secondary and not primary. But the material for such an investigation was not available.

It is interesting to observe that the Pterygo-quadrate is fixed in Cyclostomata. In *Petromyzon* (Parker) the Pterygo-quadrate is continuous with the Chondrocranium by a basal process, and by one with the ethmoid region of the skull. In *Myxine* (Cole) the Pterygo-quadrate is continuous with the Trabecula by two bars, and its anterior continuation—the palatine—by a third bar. In *Bdellostoma* (Ayers and Jackson) the Pterygo-quadrate articulates with the auditory capsule, is continuous with the palatine, and from the junction, projects a process which is continuous with the Trabecula.

It would thus appear that, whatever the genealogical relationship of the Cyclostomata and Gnathostomata may be, the former have sprung from forms with a fixed Pterygo-quadrate.

I have the pleasure of thanking Dr Henderson for the loan of an embryo of *Scyllium* and a larva of *Amblystoma*; D. P. F. Murray, Esq. for embryos of *Heterodontus*; Dr Bancroft for embryos of *Ceratodus*; Prof. de Lange for larvae of *Bombinator* and *Ichthyophis*; Dr Dunn for larvae of *Desmognathus*, *Spelerpes* and *Plethodon*; Prof. Sewertzoff and Prof. Schmalhausen for larvae of *Salamandrella* and *Ranodon*, and the latter also for adult specimens of both these Urodeles.

I am also indebted to Mr Emery, laboratory steward, for efficient help in making the models, and to Miss Cross for the drawings of them. The expenses were met by a grant from the Colston Research Society.

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DESCRIPTION OF FIGURES

In any figures of sections of the same specimen the lowest number indicates the most anterior or the most dorsal section, as the case may be.

Scyllium canicula. Figs. 1–20.

Figs. 1–5. Embryo 14 mm. long, horizontal sections.
Figs. 6, 7. Embryo 17 mm. long; model fig. 6 seen from without; fig. 7 seen from within.
Figs. 8–11. Embryo 20 mm. long, horizontal sections.
Fig. 12. Embryo 23 mm. long, model seen from without.
Fig. 13. Embryo 29 mm. long, transverse section. The section is slightly oblique and cuts the primordium of the spiracular cartilage on the left side, whilst it is in front of it on the right.
Figs. 14–17. Embryo 35 mm. long, transverse sections.
Figs. 18–20. Embryo 53 mm. long, transverse sections.

Squalus acanthias. Figs. 21–23.

Figs. 21–23. Embryo 22 mm. long, horizontal sections; fig. 21 is the most dorsal.

Heterodontus. Figs. 24, 25.

Figs. 24, 25. Embryo 47 mm. long, drawings of model. Fig. 24 is of the left side; fig. 25 of the right side showing the mandibular muscles. Anteriorly the cartilage passes into procartilage at the dotted line, and this gradually into connective tissue. The anterior limit of the Chrondrocranium is thus indefinite. The primordium of the spiracular cartilage and the upper part of the auditory capsule is also procartilaginous. There is no post-orbital process.

Amia calva. Figs. 26–28.

Fig. 26. Embryo 6·5 mm. long, drawing of model showing the mandibular and hyoid muscles from the side.
Fig. 27. Embryo 7·5 mm. long, the same.
Fig. 28. Embryo 8·5 mm. long, transverse section.

Ceratodus forsteri. Figs. 29–40.

Figs. 29, 30. Embryo 6 mm. long, horizontal sections.
Figs. 31, 32. Embryo 9 mm. long, horizontal sections.
Fig. 33. Embryo 11 mm. long, horizontal sections.
Figs. 34–36. Embryo 11 mm. long, transverse section. There is a distance of ·08 mm. between figs. 34 and 35. Fig. 36 depicts the section next behind that in fig. 35.
Fig. 37. Embryo 12 mm. long, transverse section.
Figs. 38, 39. Embryo 12·5 mm. long, drawings of model of ocular muscles. Fig. 38 from above; fig. 39 from below.
Fig. 40. Embryo 19 mm. long, horizontal section. The section is slightly oblique, sloping from the middle line outwards and slightly downwards.

Amblystoma punctatum. Fig. 41.

Fig. 41. Larva 13·5 mm. long, horizontal section.

Desmognathus fuscus. Fig. 42.

Fig. 42. Larva 19 mm. long, transverse section.

Plethodon cinereus. Figs. 43, 44.

Fig. 43. Adult 25 mm. long, transverse section.
Fig. 44. Adult 49 mm. long, transverse section.

Salamandrella Keyserlingii. Figs. 45–50.

Fig. 45. Larva 13·5 mm. long, horizontal section.
Figs. 46, 47. Larva 17 mm. long, drawings of model of chondrocranium.
Fig. 48. Larva 17 mm. long, transverse section.
Fig. 49. Larva 22·5 mm. long, transverse section.
Fig. 50. Larva 34 mm. long, transverse section.

Ranodon sibiricus. Figs. 51, 52.

Figs. 51, 52. Larva 25 mm. long, drawings of model of chondrocranium.

Menopoma alleghaniense. Figs. 53–63.

Figs. 53–55. Larva 15 mm. long, horizontal sections; 53 is the most dorsal.
Figs. 56–58. Larva 16 mm. long, horizontal sections; 56 is the most dorsal.
Figs. 59, 60. Larva 20 mm. long, horizontal sections; 59 is the more dorsal.
Fig. 61. Larva 20 mm. long, drawing of model of masticatory muscles from the outside.
Fig. 62. Larva 24 mm. long, transverse section.
Fig. 63. Larva 28 mm. long, transverse section.

Necturus maculatus. Figs. 64–66.

Figs. 64, 65. Embryo 25 mm. long, transverse section; 64 is the more anterior.
Fig. 66. Embryo 30 mm. long, drawing of model of chondrocranium from below.

Rana temp. Figs. 67–79.

Figs. 67, 68. Larva 8 mm. long, horizontal sections; 67 is the more dorsal.
Figs. 69, 70. Larva 9 mm. long, sagittal sections; 69 is the more external.
Fig. 71–75. Larva 9½ mm. long, transverse sections; 71 is the most anterior.
Fig. 76. Larva 10 mm. long, transverse section.
Fig. 77. Larva 11 mm. long, transverse section.
Fig. 78. Larva 20 mm. long, transverse section.
Fig. 79. Larva 21 mm. long, transverse section.

Bombinator. Figs. 80–83.

Figs. 80–83. Larva 8 mm. long, horizontal sections; 80 is the most dorsal.

Siphonops braziliensis. Figs. 84–89.

Figs. 84–89. Larva 70 mm. long, transverse sections; 84 is the most anterior.

Ichthyophis glutinosus. Figs. 90–103.

Figs. 90, 91. Larva 28·5 mm. long, drawings of model of chondrocranium; 90 from below; 91 from outside.
Figs. 92, 93. Larva 28·5 mm. long, drawings of model of masticatory muscles; 92 from outside; 93 from inside.
Fig. 94. Larva 28·5 mm. long, transverse section.
Figs. 95–97. Larva stage 2 (of development intermediate between the 28·5 and 35 mm. larvae), transverse sections; 95 is the most anterior.
Figs. 98–102. Larva 35 mm. long, transverse sections; 98 is the most anterior: there is a distance of ·04 mm. between 100 and 101, and of ·05 mm. between 101 and 102.
Fig. 103. Larva 59 mm. long, transverse section.

ABBREVIATIONS

Add. mand.	Adductor mandibulae
ant. orb. proc.	antorbital process
asc. proc. Quad.	ascending process of Quadrate
aud. caps.	auditory capsule
basal proc. Quad.	basal process of Quadrate
Branch. i.	Branchiale i.
Col. auris	Columella auris
Comp. gl. orbit.	Compressor glandulae orbitalis
Constr. i. dors.	Constrictor i. dorsalis
Dep. mand.	Depressor mandibulae
Duct. endolymph.	Ductus endolymphaticus
g. max. mand. v.	ganglion maxillo-mandibulare v.
Gass. g.	Gasserian ganglion
genic. g. vii.	geniculate ganglion vii.
geniocorac.	Genio-coracoideus
hyoid m. pl.	hyoid muscle plate
Intermand.	Intermandibularis
Keratohy. c.	Keratohyal cartilage

lat. proc. basal pl.	lateral process of basal plate
Lev. bulbi	Levator bulbi
Lev. mand. ant.	Levator mandibulae anterior
Lev. mand. ext.	Levator mandibulae externus
Lev. m. ant. {subext. / lat. / art.}	primordium of Levatores mandibulae anterior subexternus prim. of lateralis and articularis
Lev. mand. post.	Levator mandibulae posterior
Lev. m. post. prof.	Levator mandibulae posterior profundus
Lev. m. post. superf.	Levator mandibulae posterior superficialis
Lev. quad.	Levator quadrati
ling. m.	lingual muscles
mand. gloss.	Mandibulo-glossus
mand. m. pl.	mandibular muscle plate
mast. m. pl.	masticatory muscle plate
max. pal. b.	maxillo-palatine bone
N. alv. v.	Nervus alveolaris v.
N. alv. vii.	Nervus alveolaris vii.
N. bucc. vii.	Nervus buccalis vii.
N. hypogloss.	Nervus hypoglossus
N. mand. v.	Nervus mandibularis v.
N. max. v.	Nervus maxillaris v.
Orbit. hyoid	Orbito-hyoideus
Obliq. inf.	Obliquus inferior
Obliq. sup.	Obliquus superior
Otic pr. Quad.	Otic process of Quadrate
Pal. quad.	Palato-quadrate
Paraquad. b.	Paraquadrate bone
Pariet. b.	Parietal bone
Plan. internus	Planum
Praeorb.	Praeorbitalis
praefacial com.	praefacial commissure
praemand. som.	praemandibular somite
proc. musc. Quad.	processus muscularis of Quadrate
ptery. b.	pterygoid bone
R. alv. v.	Ramus alveolaris v.
R. alv. vii.	Ramus alveolaris vii.
R. mand. v.	Ramus mandibularis v.
R. max. v.	Ramus maxillaris v.
R. max. mand. v.	Ramus maxillo-mandibularis v.
R. oph. prof. v.	Ramus ophthalmicus profundus v.
R. oph. superf. vii.	Ramus ophthalmicus superficialis vii.
R. post N. intermand. v.	Ramus posterior of Nervus intermandibularis v.
Spir. cart.	Spiracular cartilage
Sub. arc. R. i.	Subarcualis rectus i.
Suspens. ceratohy. and Quadang.	primordium of Suspensorio-ceratohyoideus and Quadrato-angularis
Suspen. hyoid.	Suspensorio-hyoideus
Taenia marg.	Taenia marginata
Trab.	Trabecula
R. max. ext. v.	Ramus maxillaris externus v.
Tr. hyomand. vii.	Truncus hyomandibularis vii.
Roman numerals	Cranial nerves

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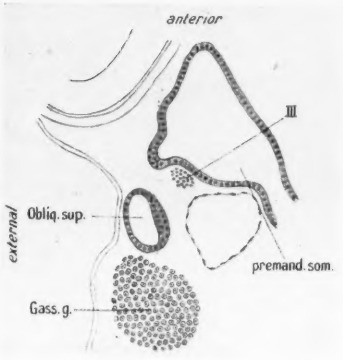

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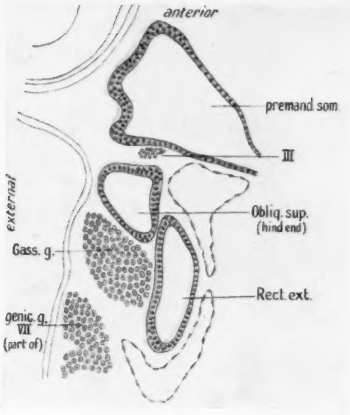

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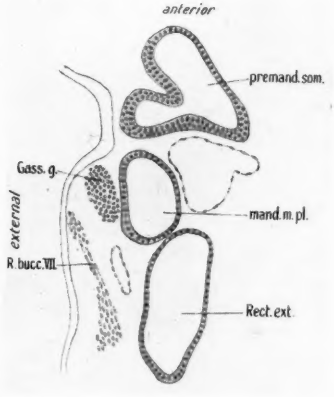

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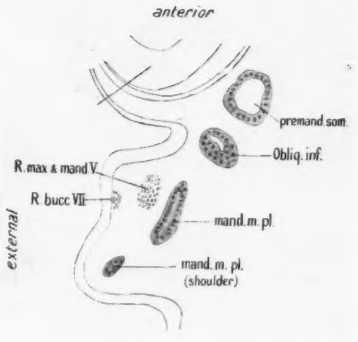

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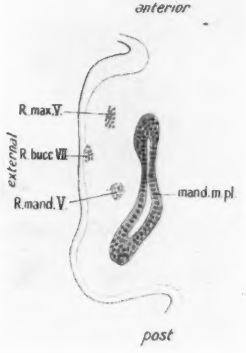

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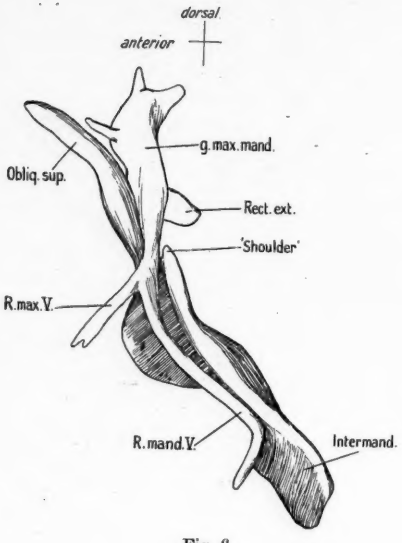

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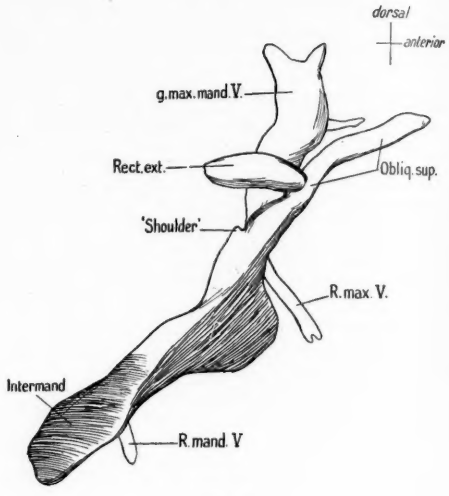

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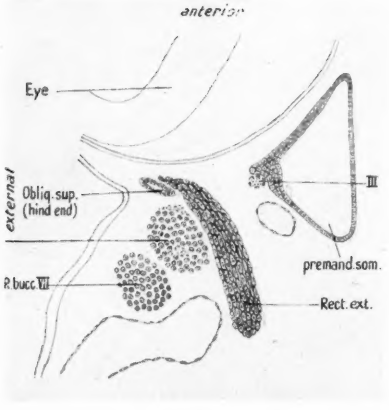

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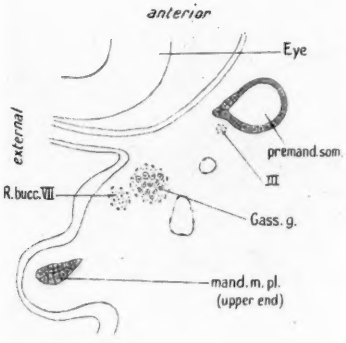

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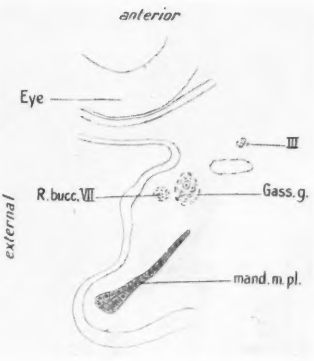

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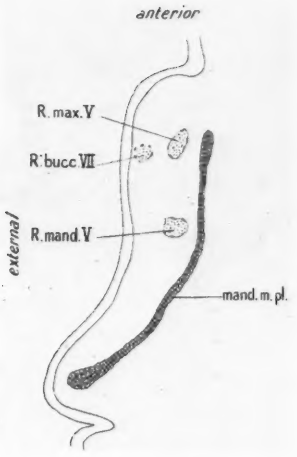

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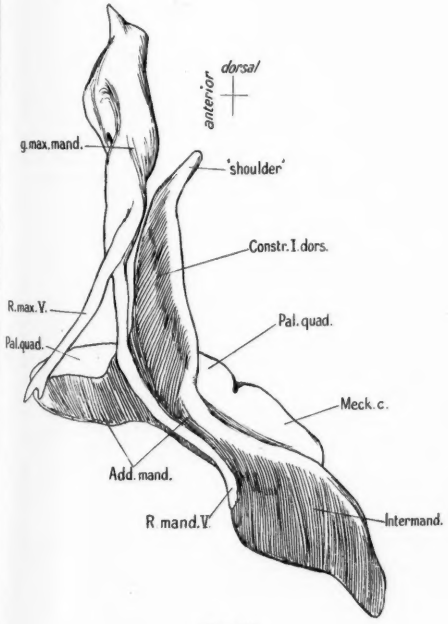

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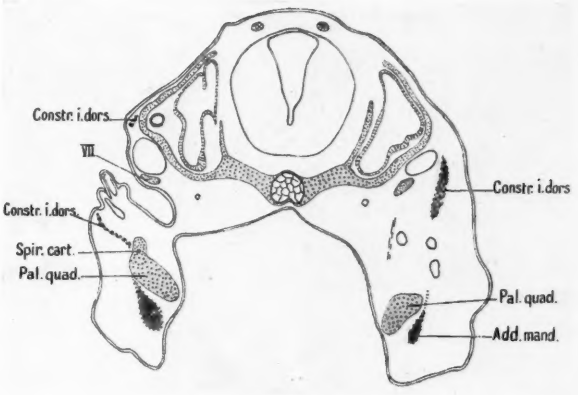

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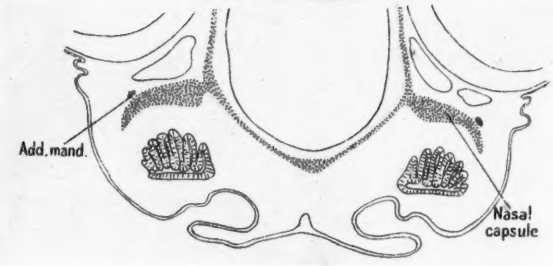

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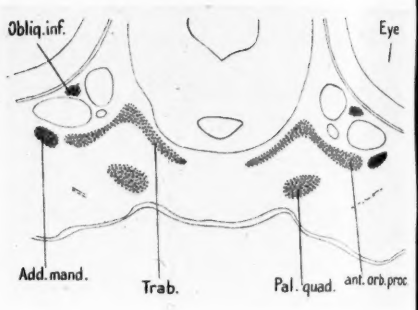

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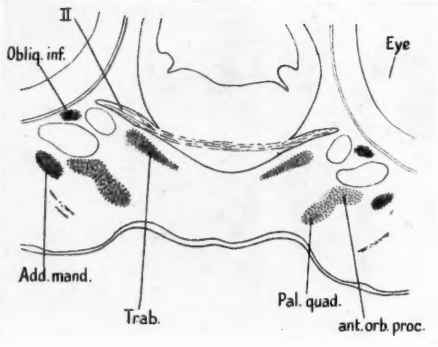

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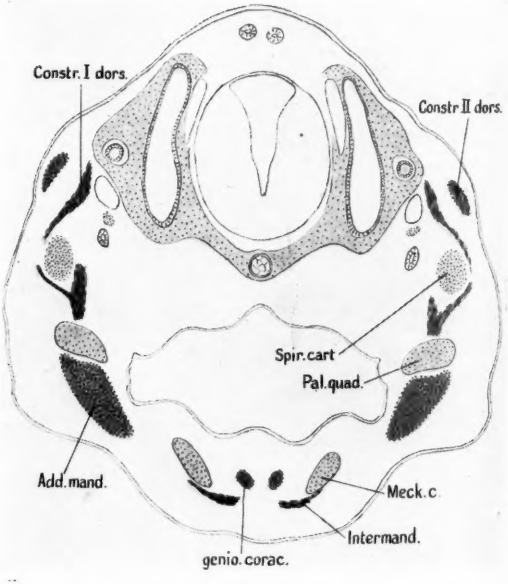

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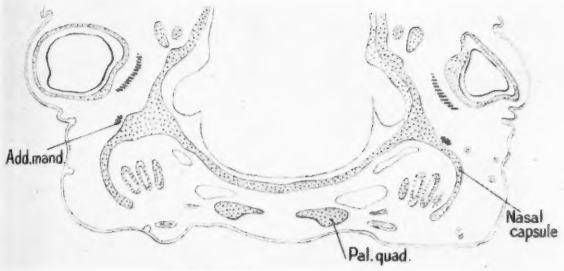

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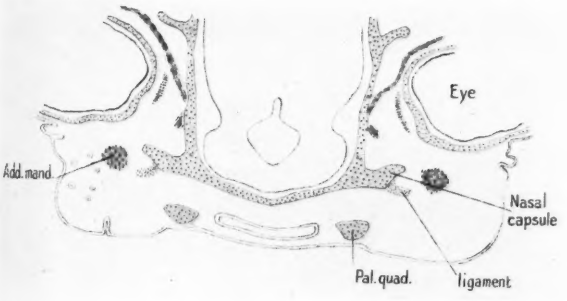

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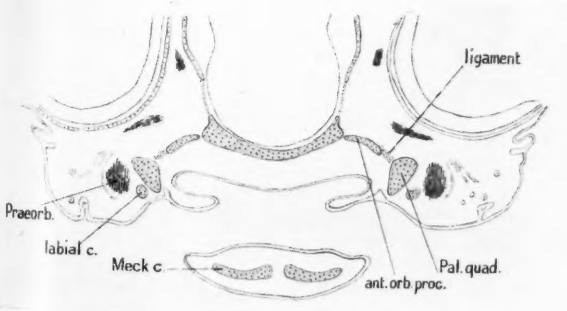

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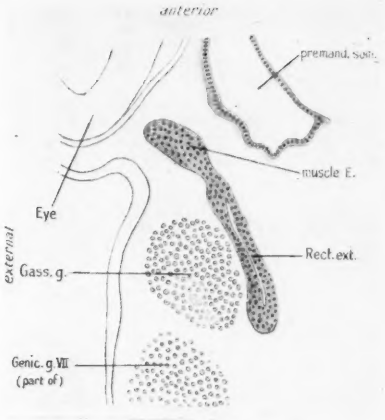

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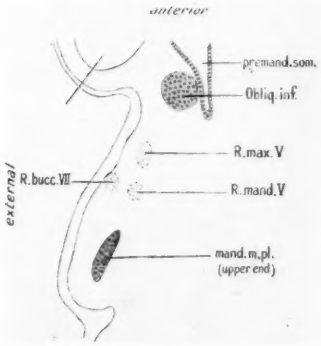
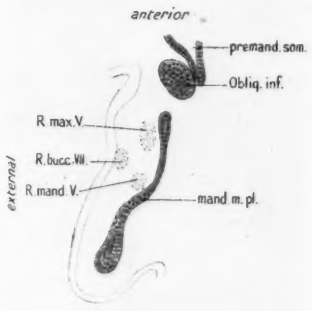


Fig. 22



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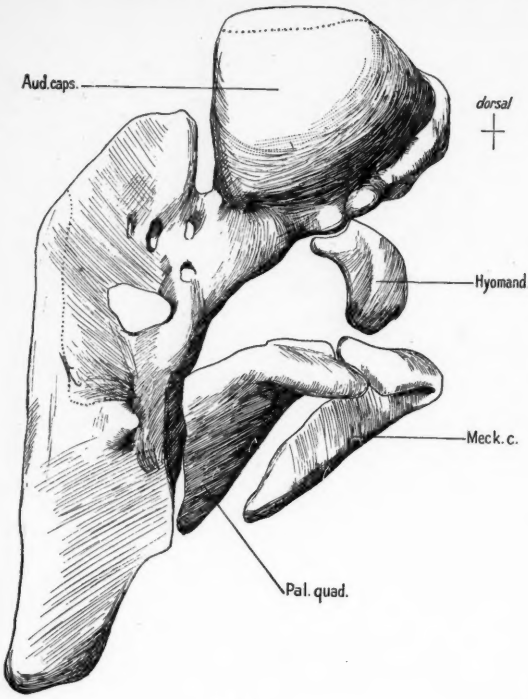

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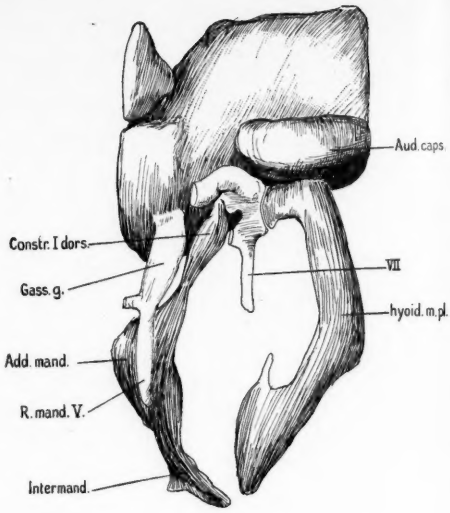

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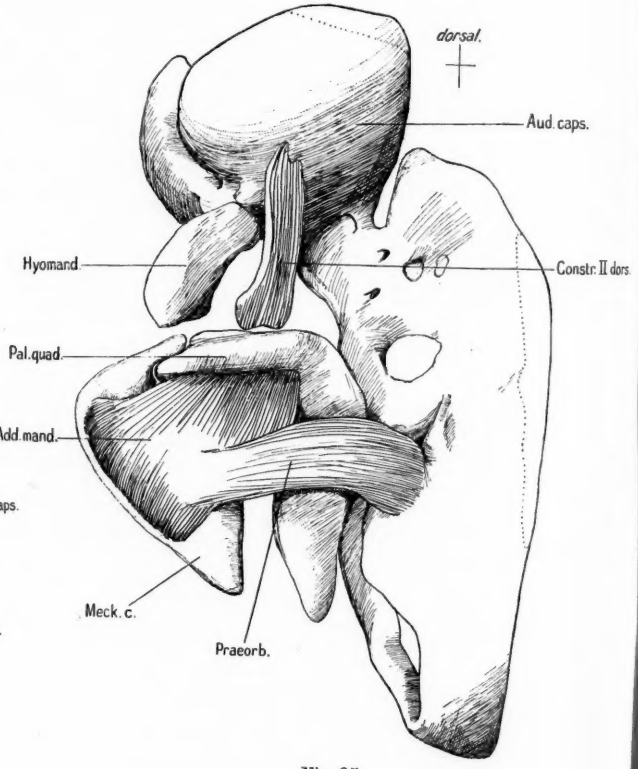

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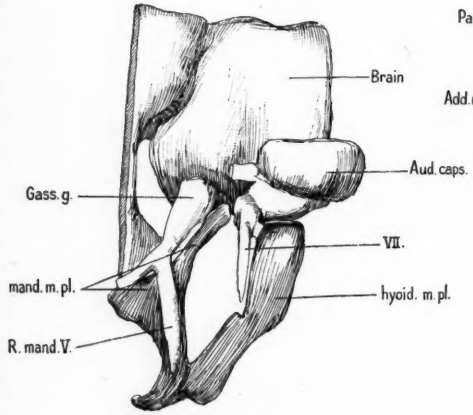

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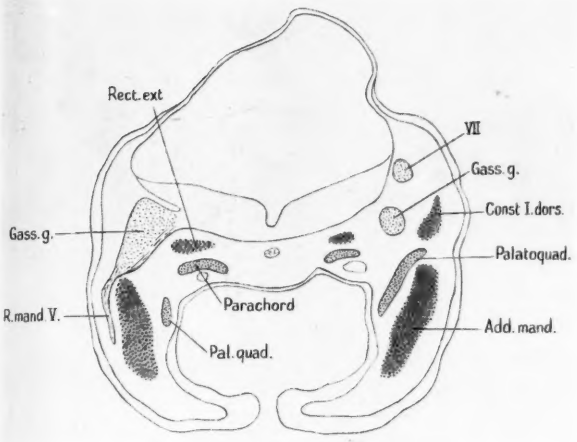

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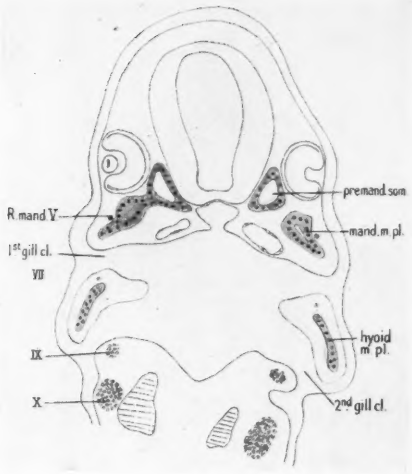

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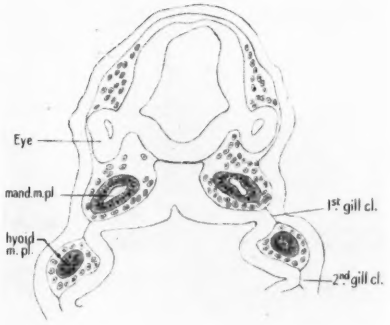

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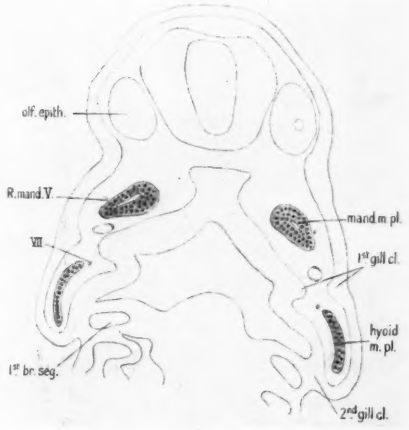

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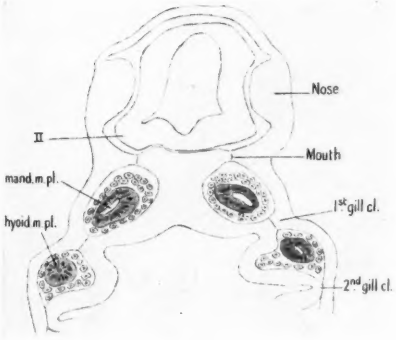

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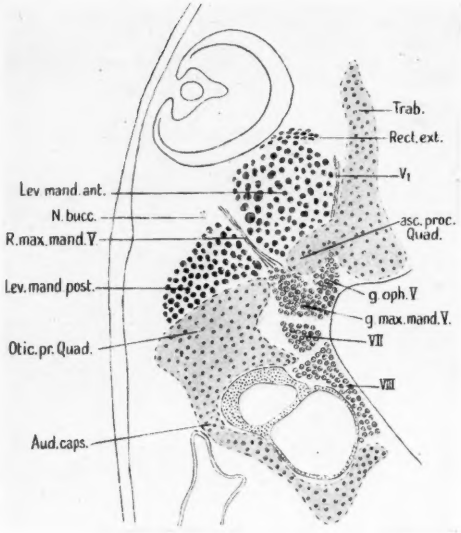

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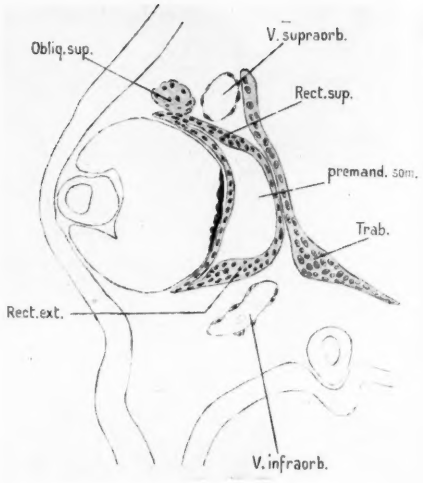

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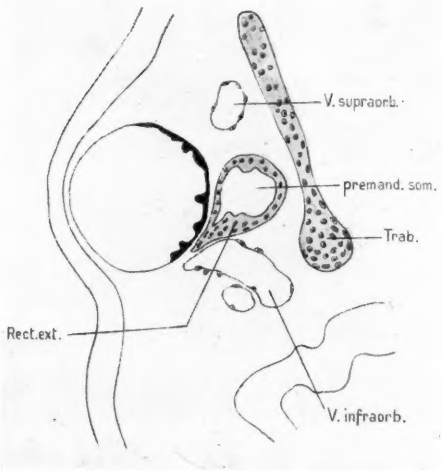

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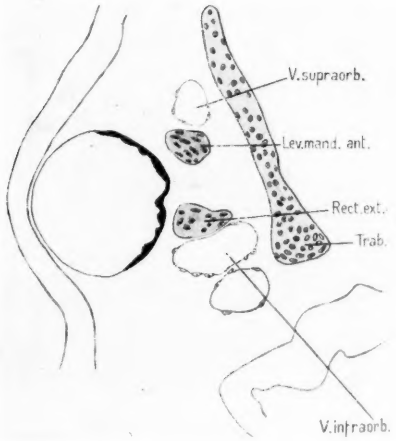

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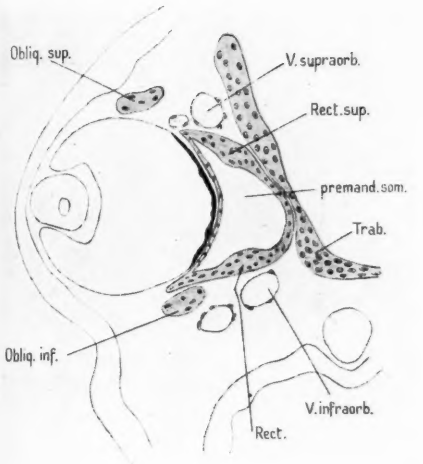

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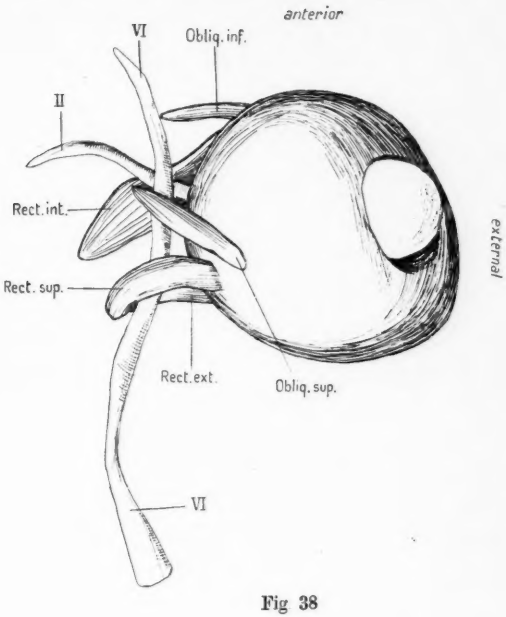

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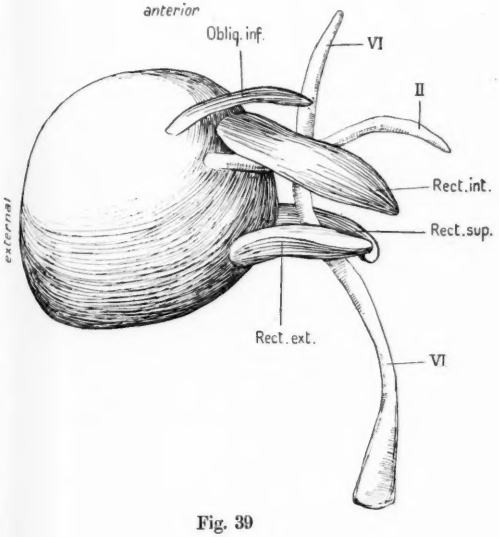

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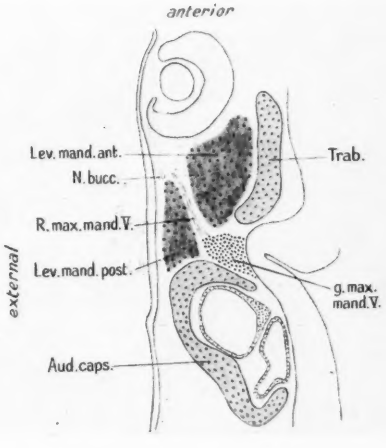

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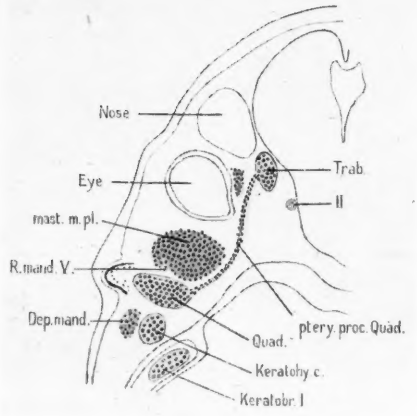

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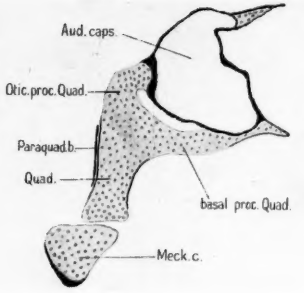

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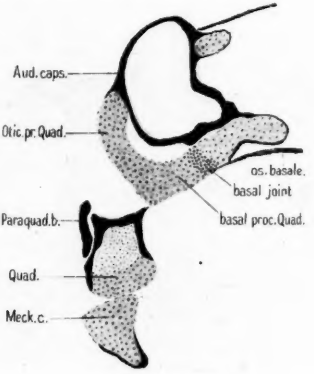

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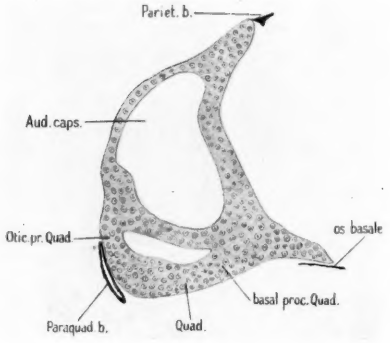

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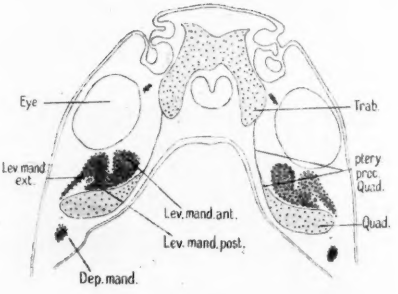

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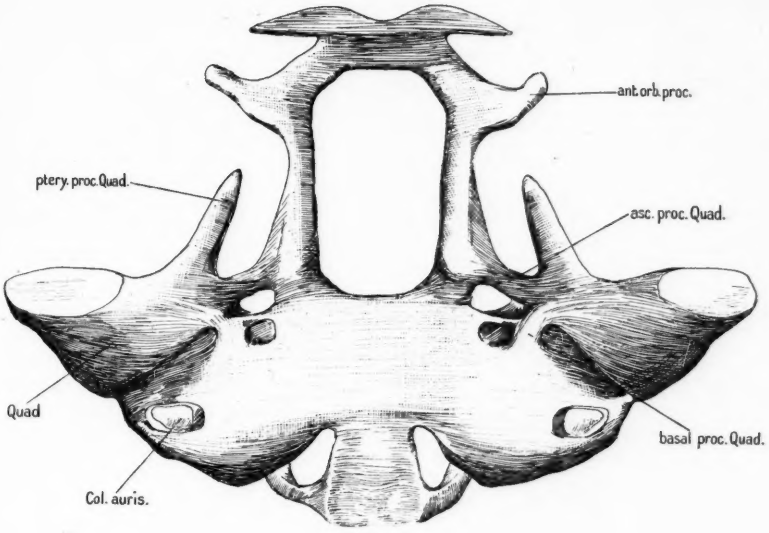
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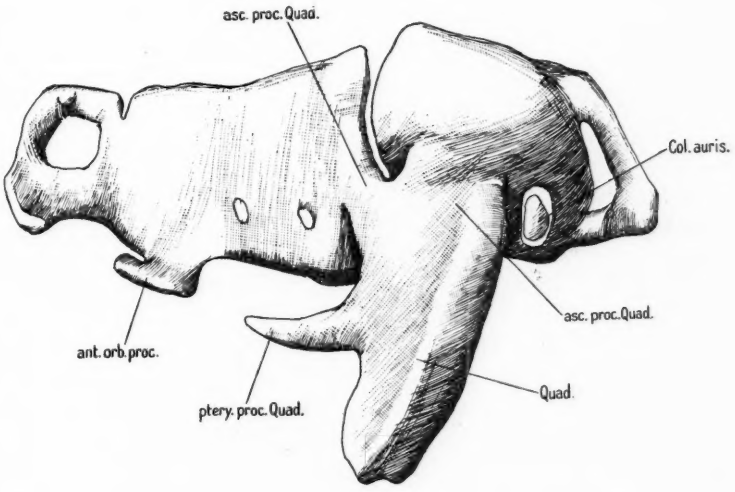
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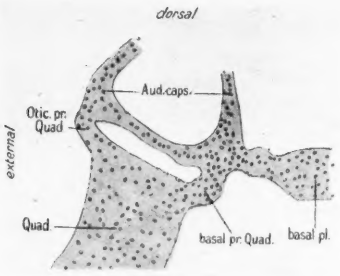
Fig. 47



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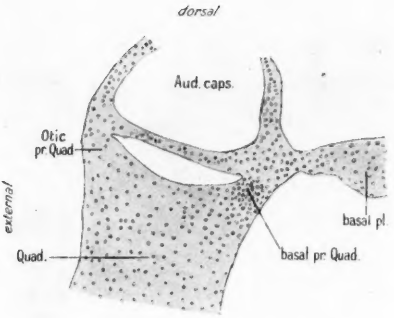

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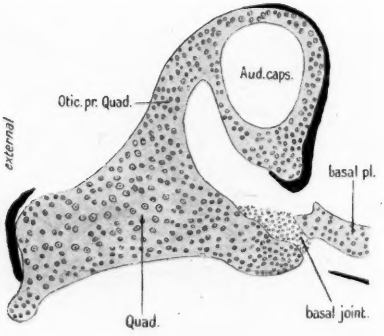

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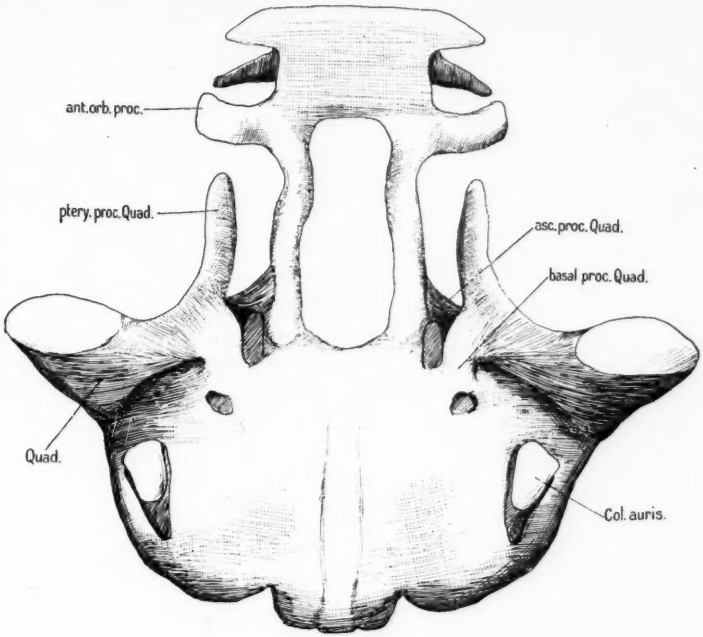
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Fig. 51

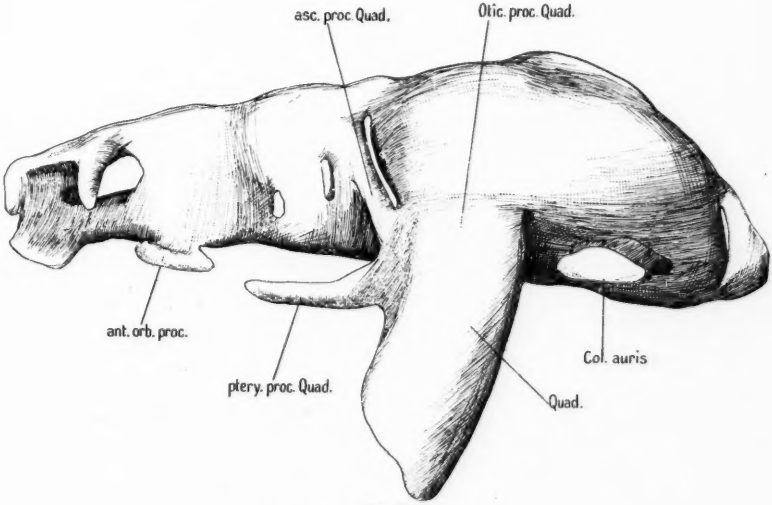
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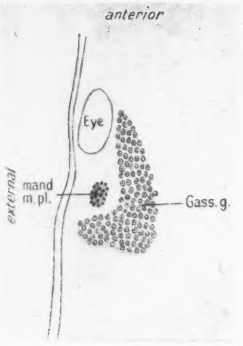
Fig. 52



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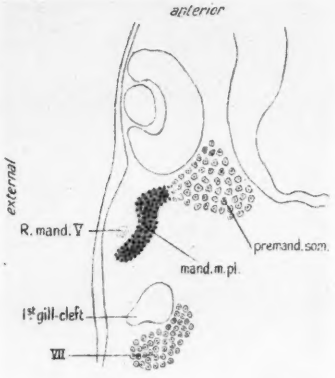

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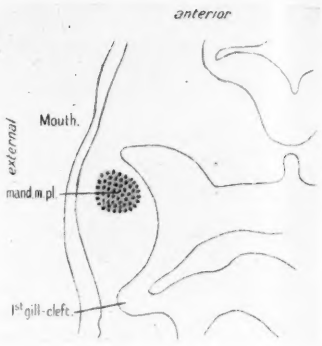

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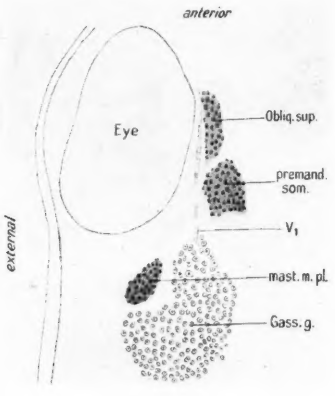

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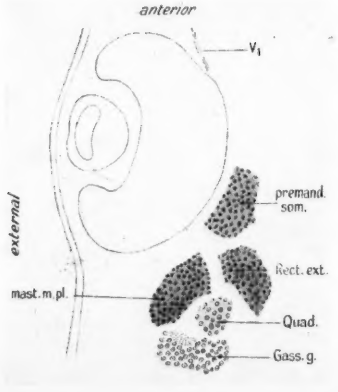

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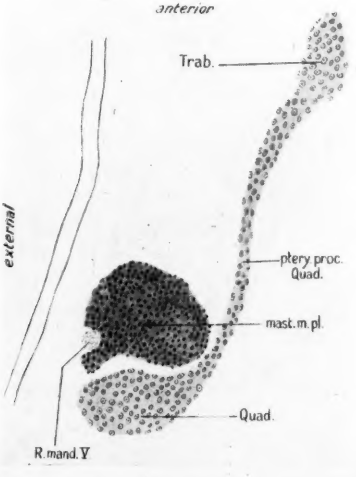

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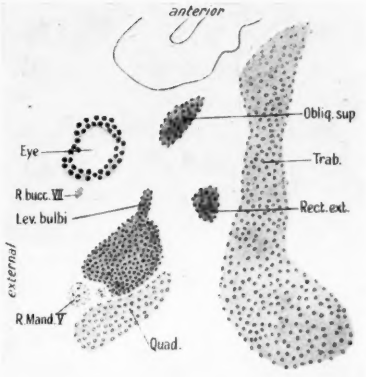

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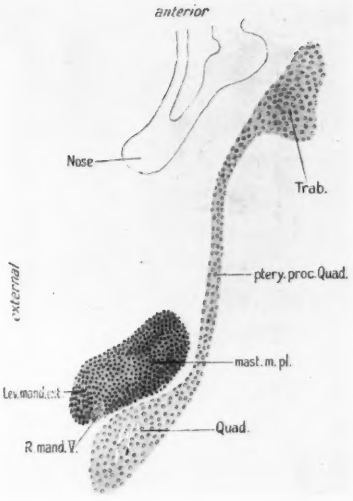

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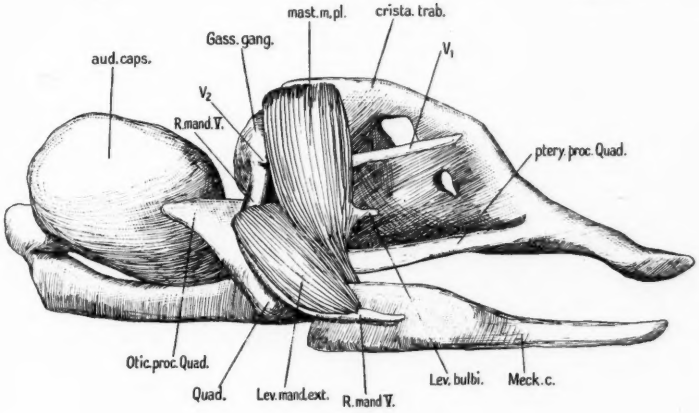

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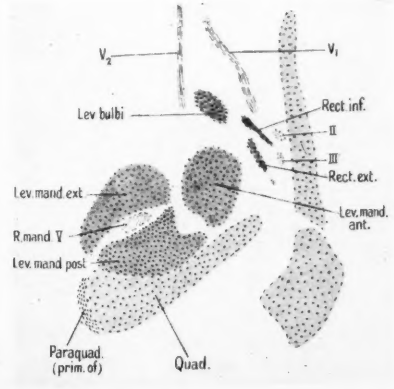

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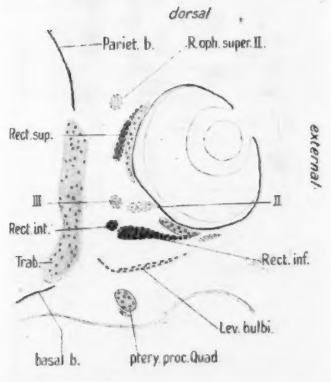

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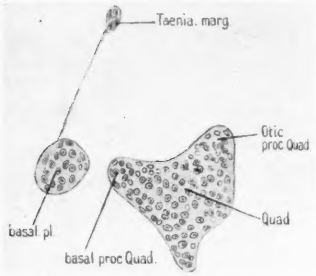

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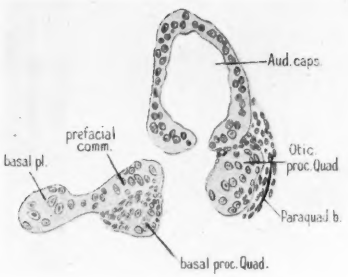

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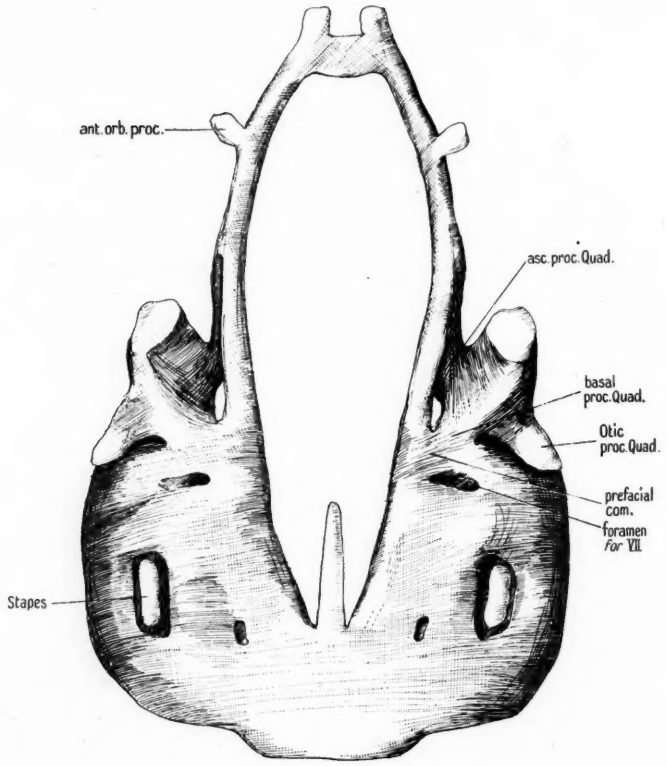

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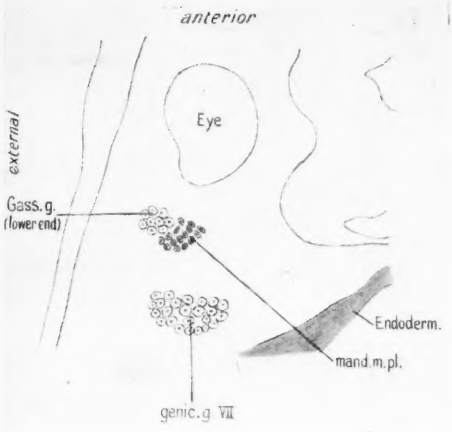

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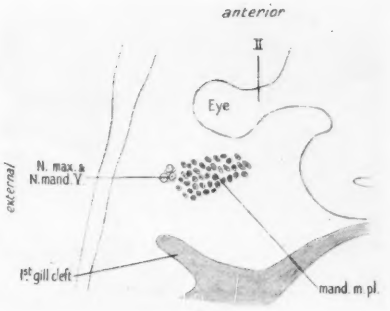

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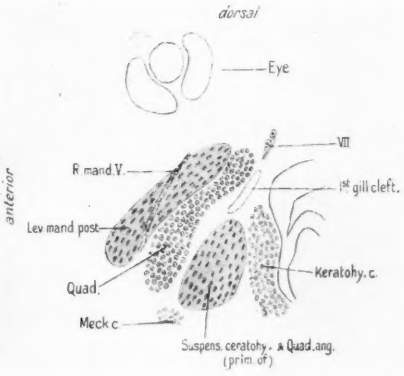

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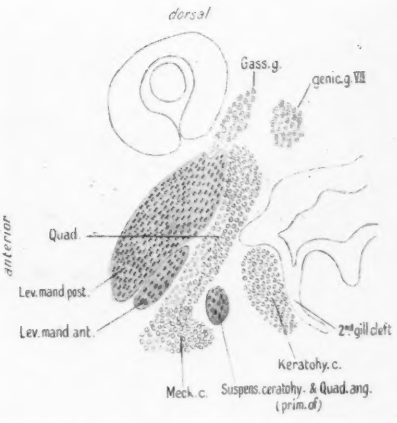

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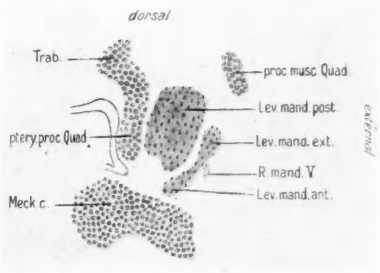

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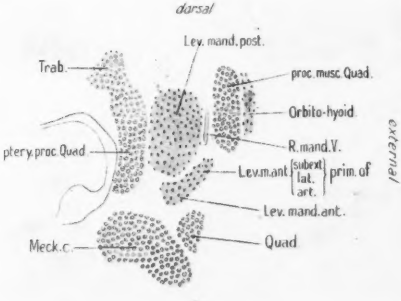

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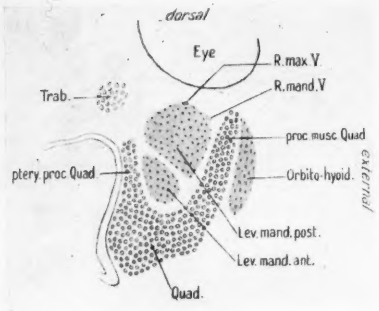
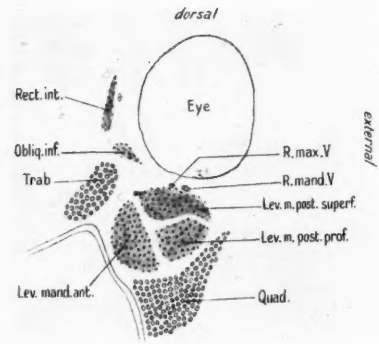


Fig. 73



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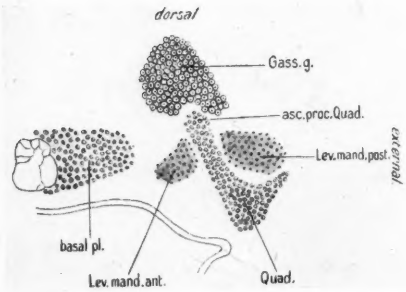


Fig. 75

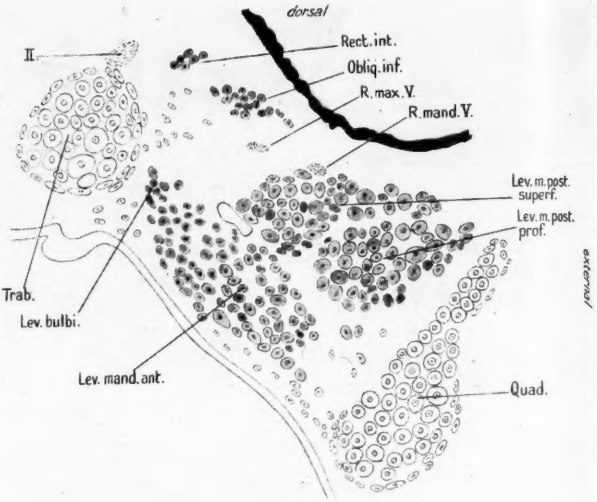


Fig. 76

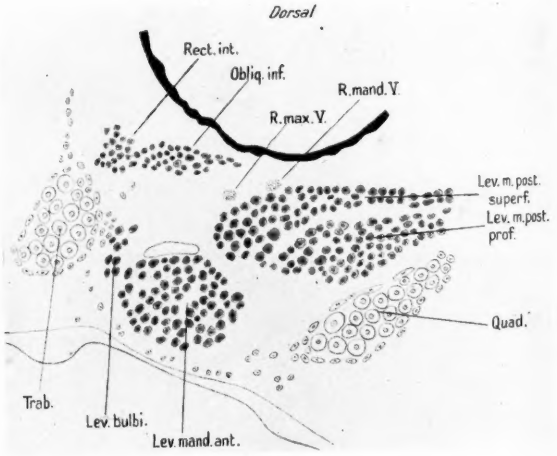
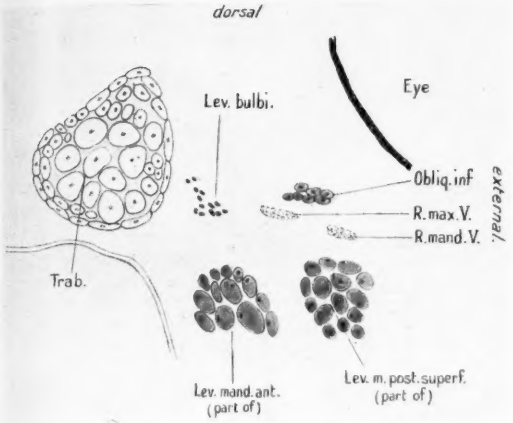


Fig. 77



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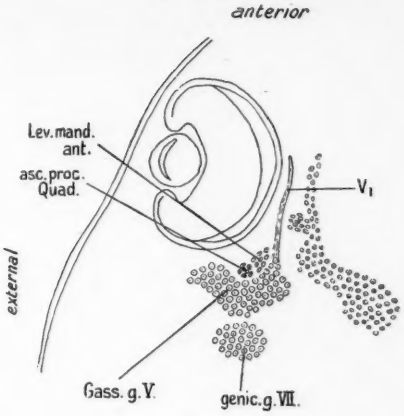


Fig. 80

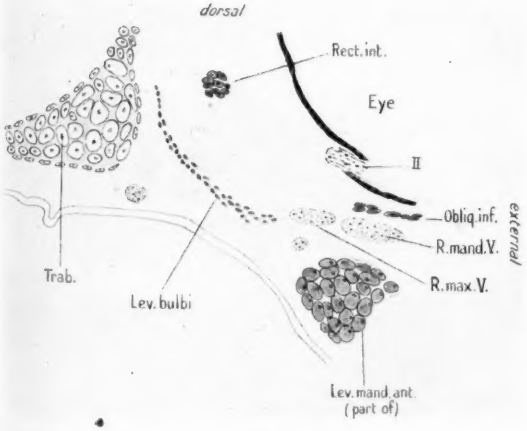
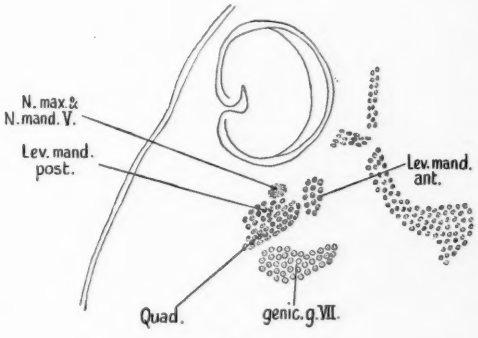


Fig. 79



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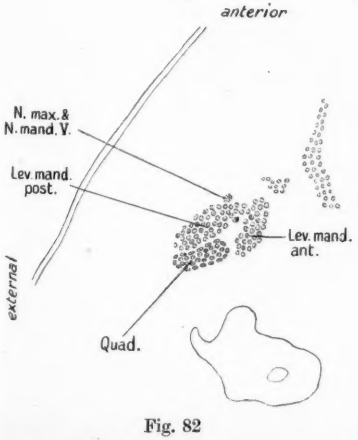

Fig. 82

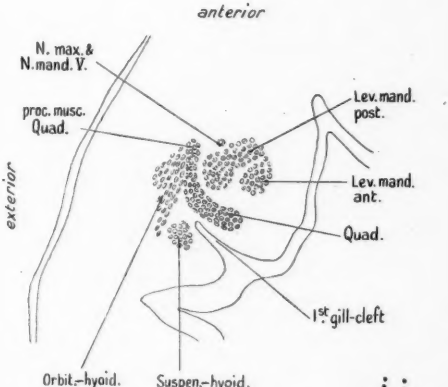

Fig. 83

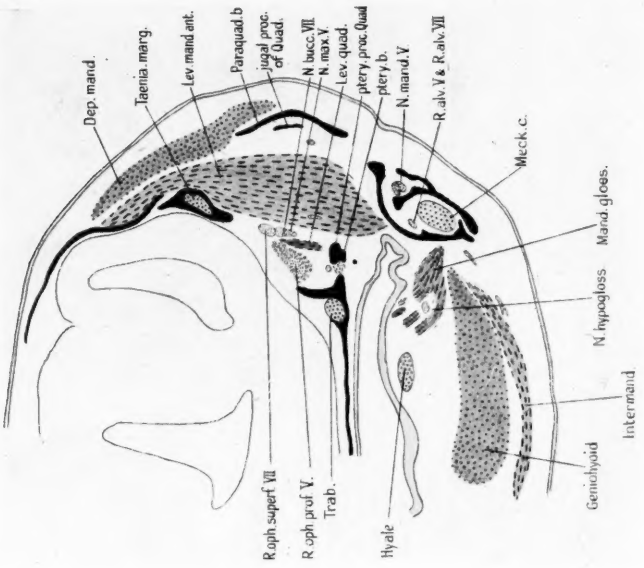
Dep. mand.
Taenia marg.
Lev. mand ant.
Paraquad.b
jugal proc. of Quad.
N. bucc. VII
N. max. V
Lev. quad.
ptery. proc. Quad
ptery. b.
N. mand. V
R. alv. V & R. alv. VII
Meck. c.
Mand gloss.
N. hypogloss
Intermand.
Geniohyoid
R. oph. superf. VII
R. oph. prof. V.
Trab.
Hyale

Fig. 85

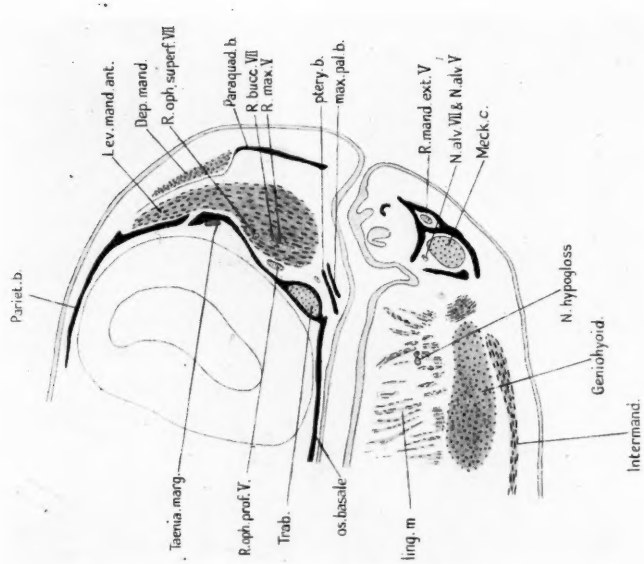
Pariet. b.
Lev. mand. ant.
Dep. mand.
R. oph. superf. VII
Paraquad. b.
R. bucc. VII
R. max. V
ptery. b.
max. pal b.
R. mand ext. V
N. alv. VII & N. alv. V
Meck. c.
N. hypogloss
Geniohyoid
Intermand.
Taenia. marg.
R. oph. prof. V.
Trab.
os. basale
ling. m

Fig. 84

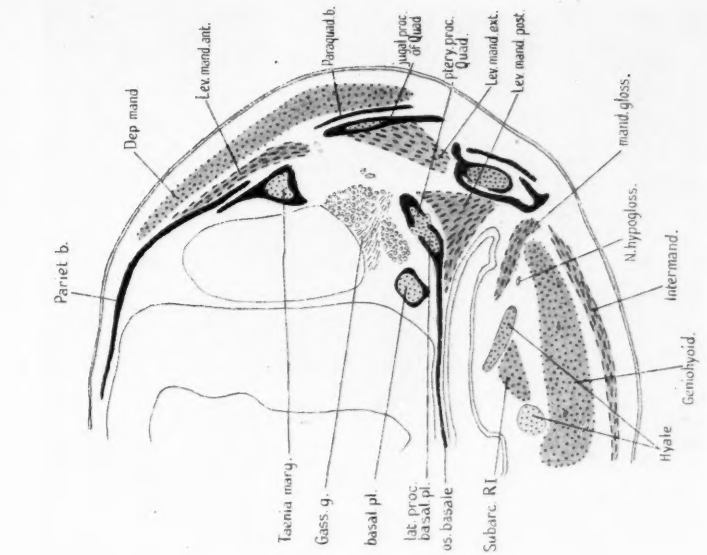
Pariet. b.
Dep mand
Lev. mand. ant.
Paraquad b.
jugal proc of Quad
ptery. proc. Quad.
Lev mand ext.
Lev mand post.
mand gloss.
N. hypogloss.
Intermand.
Geniohyoid.
Hyale
Taenia marg.
Gass. g.
basal pl.
lat. proc. basal pl.
os. basale
Subarc. RI

Fig. 87

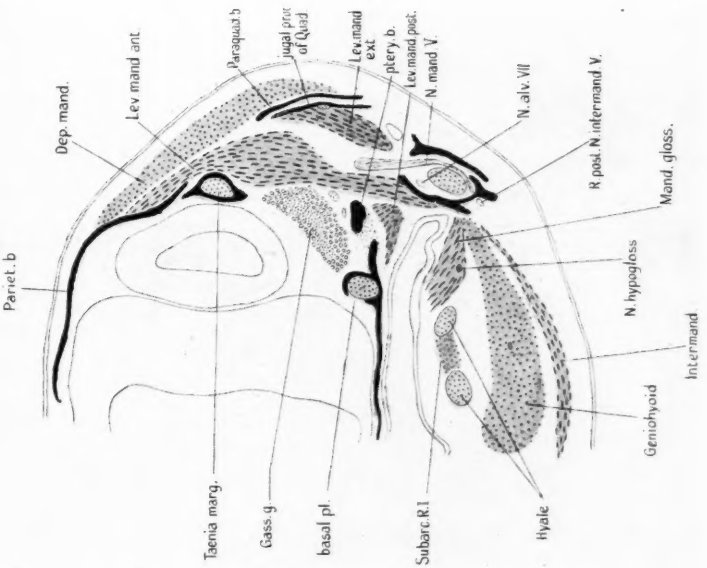
Pariet. b
Dep. mand.
Lev mand ant.
Paraquad b
jugal proc of Quad
Lev.mand ext.
ptery. b.
Lev mand post.
N. mand V.
N. alv. VII
R. post. N. intermand V.
Mand. gloss.
N. hypogloss
Intermand
Geniohyoid
Hyale
Taenia marg.
Gass. g
basal pl.
Subarc. R.I

Fig. 86

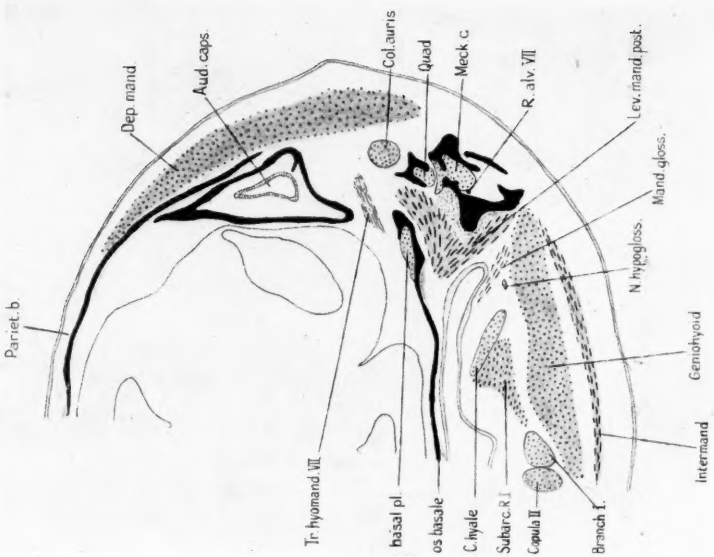
Pariet. b
Dep. mand
Aud. caps.
Col. auris
Quad
Meck. c
R. alv. VII
Lev. mand. post.
Mand. gloss.
N. hypogloss.
Geniohyoid
Intermand
Tr. hyomand. VII
basal pl.
os basale
C. hyale
Subarc. R. I
Copula II
Branch I.

Fig. 89

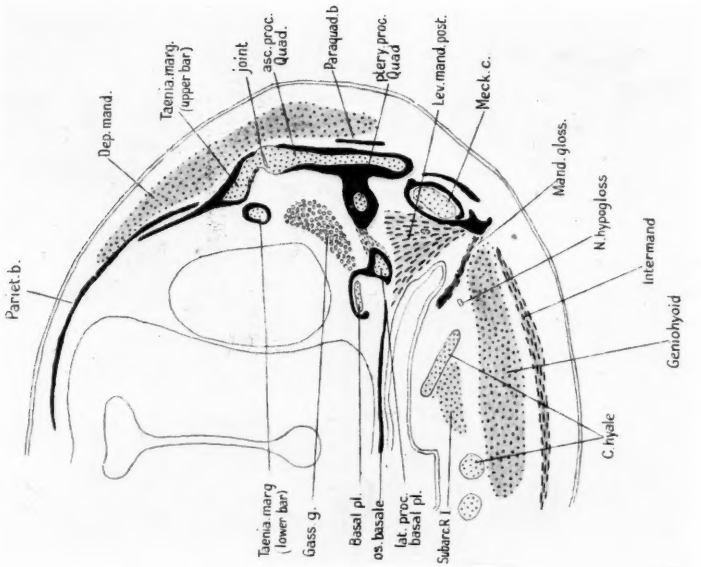
Pariet. b.
Dep. mand.
Taenia marg. (upper bar)
joint
asc. proc. Quad.
Paraquad. b
ptery. proc. Quad
Lev. mand. post.
Meck. c.
Mand. gloss.
N. hypogloss
Intermand
Geniohyoid
C. hyale
Taenia marg (lower bar)
Gass. g.
Basal pl.
os. basale
lat. proc. basal pl.
Subarc. R I

Fig. 88

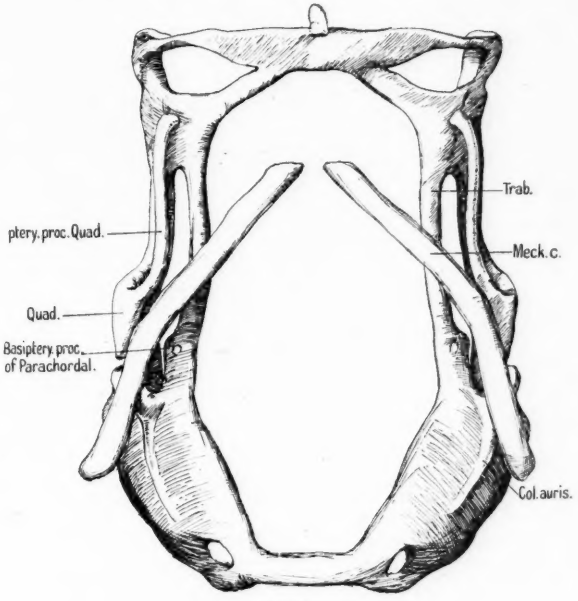
Trab.
ptery. proc. Quad.
Meck. c.
Quad.
Basiptery. proc. of Parachordal.
Col. auris.

Fig. 90

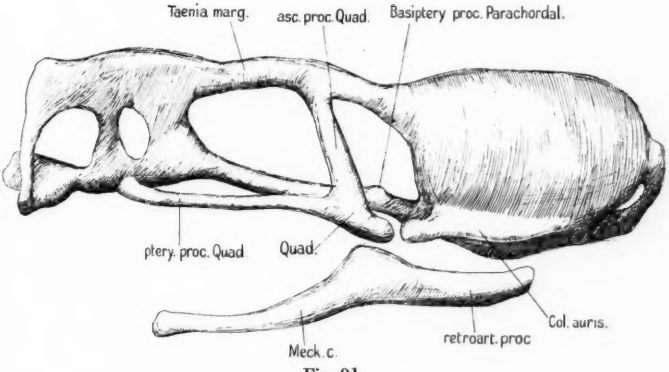
Taenia marg.
asc. proc. Quad.
Basiptery proc. Parachordal.
ptery. proc. Quad
Quad.
Col. auris.
retroart. proc
Meck. c.

Fig. 91

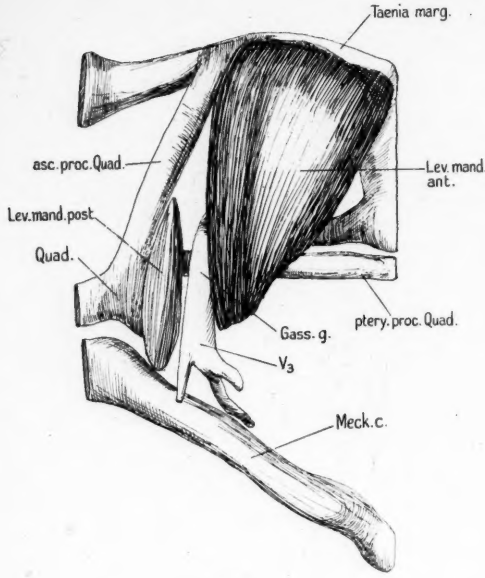

Fig. 92

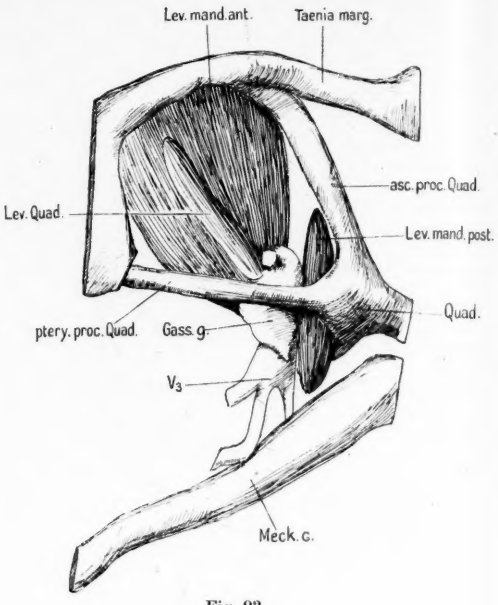

Fig. 93

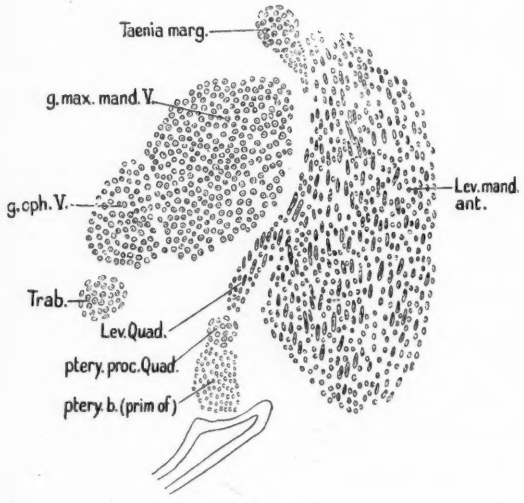

Fig. 94

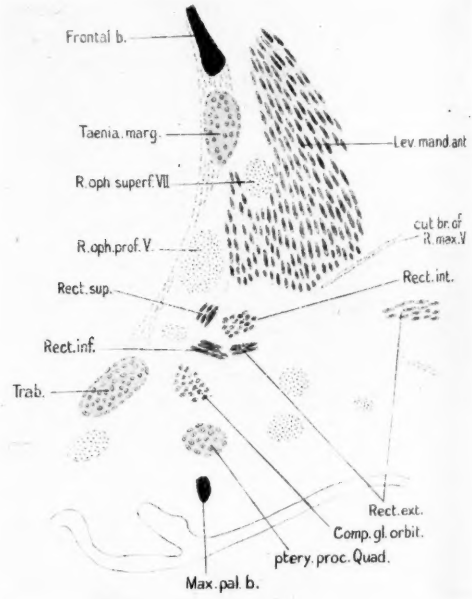

Fig. 95

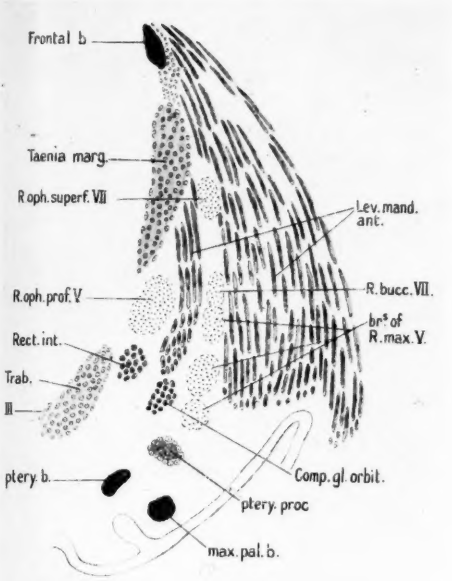

Fig. 96

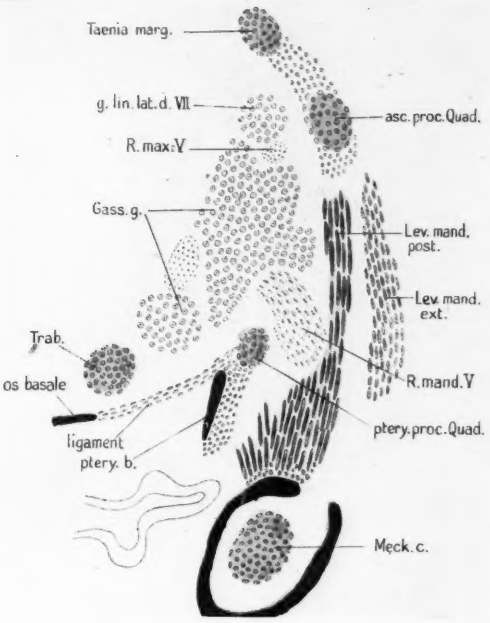

Fig. 97

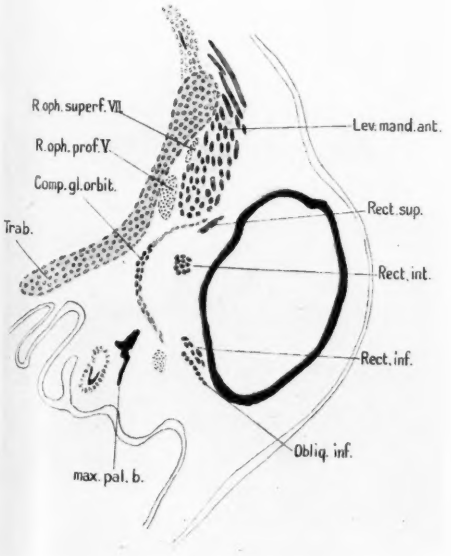

Fig. 98

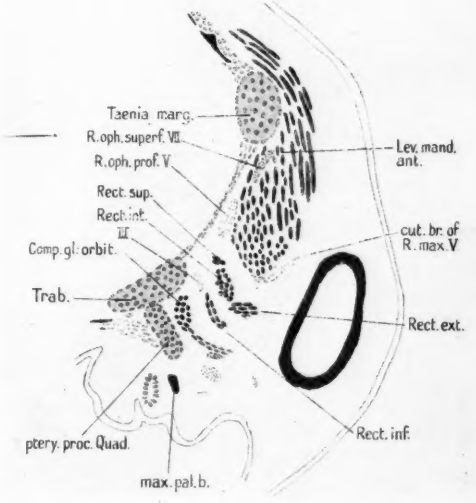

Fig. 99

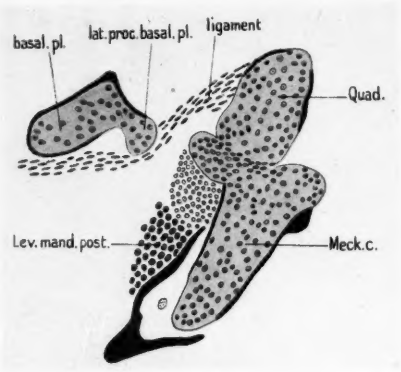

Fig. 100

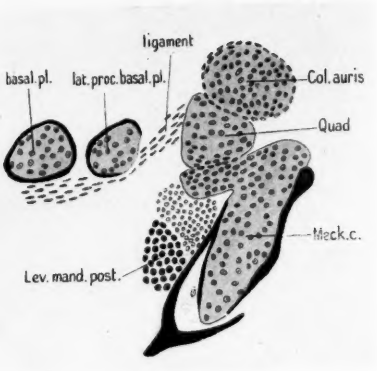

Fig. 101

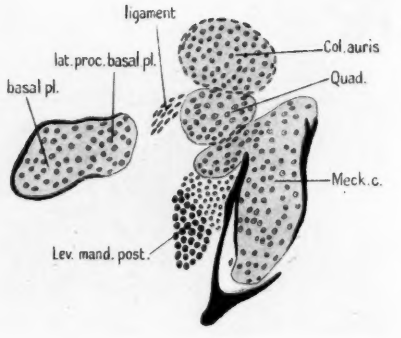

Fig. 102

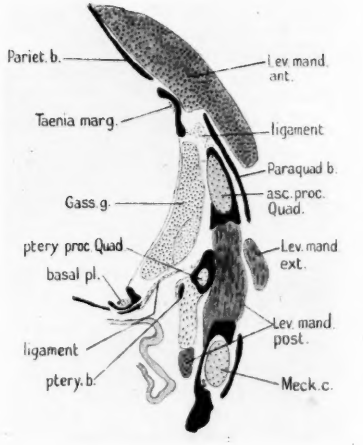

Fig. 103

THE ANOMALOUS RIGHT SUBCLAVIAN ARTERY CONSIDERED IN THE LIGHT OF RECENT FINDINGS IN ARTERIAL DEVELOPMENT; WITH A NOTE ON TWO CASES OF AN UNUSUAL RELATION OF THE INNOMINATE ARTERY TO THE TRACHEA

By JOHN CAIRNEY, M.B., Ch.B.

From the Department of Anatomy, University of Otago, New Zealand

I. THE ANOMALOUS RIGHT SUBCLAVIAN ARTERY: REPORT OF TWO CASES, WITH REVIEW OF LITERATURE

Cases in which the right subclavian artery arises directly from the arch of the aorta are classified by Quain (1844) into four groups, according as the artery arises before the right common carotid, immediately after the right common carotid, immediately after the left common carotid, or after the left subclavian. Cases of the fourth type appear to be not uncommon. Quain himself observed four cases in the examination of nearly 1000 subjects. Bradley (1871) observed two cases in 120 subjects. The third annual report of the committee of collective investigation presented by Thomson (1893) gave the incidence of the anomaly as 5 in 500, while, according to Gould (1909), the frequency has been variously estimated as 0·4 to 0·8 per cent. Harvey (1917) observed two cases in 237 subjects; Hudson (1921), 1 in 70; Goldbloom (1922), 4 in 225; and De Garis (1923), 1 in 139. In this department, the condition has been observed twice in the examination of 203 subjects. Holzapfel, whose paper I have unfortunately not been able to consult, collected (in 1899) 196 cases of the anomaly, the earliest being recorded by Bohmer in 1741; Holzapfel himself added four further cases, and Hudson (1921) mentions that he has been able to find 25 additional cases recorded in the present century. The literature at my disposal includes six further cases, one reported by Hudson, four by Goldbloom (1922), and one by De Garis (1923), bringing the total number of published cases up to at least 231.

Smith (1891) reports the occurrence of the same anomaly in the rabbit; he found it once in the examination of about 700 specimens. In this case, the right subclavian arose from the dorsal aspect of the arch of the aorta at the point where the aorta began to descend, and passed to the right dorsal to the oesophagus.

In the human subject, the anomalous right subclavian passes dorsal to the oesophagus in the great majority of cases. Indeed, certain writers in recent years have expressed doubt as to whether there has been any definitely proved case in which such a vessel passed either between the oesophagus and the trachea or ventral to the trachea.

Particulars of cases

The essential particulars of the cases recorded in the literature to which I have access are indicated for convenience in Table I. The following are particulars of the two cases which I have seen, arranged under the same headings:

Case I

Subject.—Female, aet. 56

Branches of aortic arch: Bicarotid, left subclavian, right subclavian.

Origin of right subclavian: Dorsal aspect of arch, just beyond left subclavian.

Course of right subclavian: Behind oesophagus.

Branches of subclavian: On right side, from first part, vertebral, common trunk giving rise to thyroid axis and internal mammary; from second part, costo-cervical trunk. On left side, usual.

Origin of vertebral: Usual.

Right inferior laryngeal nerve: Turned round inferior thyroid artery.

Termination of thoracic duct: Usual.

Case II

Subject.—Male, aet. 70

Branches of aortic arch: Right common carotid, left common carotid, left subclavian, right subclavian.

Origin of right subclavian: Dorsal aspect of arch, opposite third thoracic vertebra.

Course of right subclavian: Behind oesophagus.

Branches of subclavian: On right side, from first part, vertebral, superior intercostal (not costo-cervical trunk), common trunk giving rise to inferior thyroid and suprascapular, internal mammary; from second part, deep cervical; from third part, transverse cervical. On left side, from first part, vertebral, common trunk giving rise to inferior thyroid and suprascapular, internal mammary, superior intercostal, deep cervical; from second part, transverse cervical.

Origin of vertebral: Usual.

Right inferior laryngeal nerve: Passed directly to the lower border of inferior constrictor, its course being very slightly curved with the convexity downwards.

Termination of thoracic duct: Usual.

Fig. 1 represents a drawing of a cast of the specimen in the second case.

Some facts and principles in the normal transformation of the aortic-arch system

The usual descriptions of the development of the aortic-arch system as presented in our standard text-books appear to be dominated by the influence

of Rathke and to imply a belief in a strict ontogenetic recapitulation of phylogeny. The conventional diagram shows, even if the text does not definitely describe, five or six paired arterial arches present at one and the same time, and from this pattern the definitive vessels are produced by the erasing of certain fixed segments, "as though the system were made up of hard and fast units existing of and for themselves." As a natural consequence, the theories which have hitherto been advanced in connection with the anomalous right subclavian in its various aspects have similarly involved the

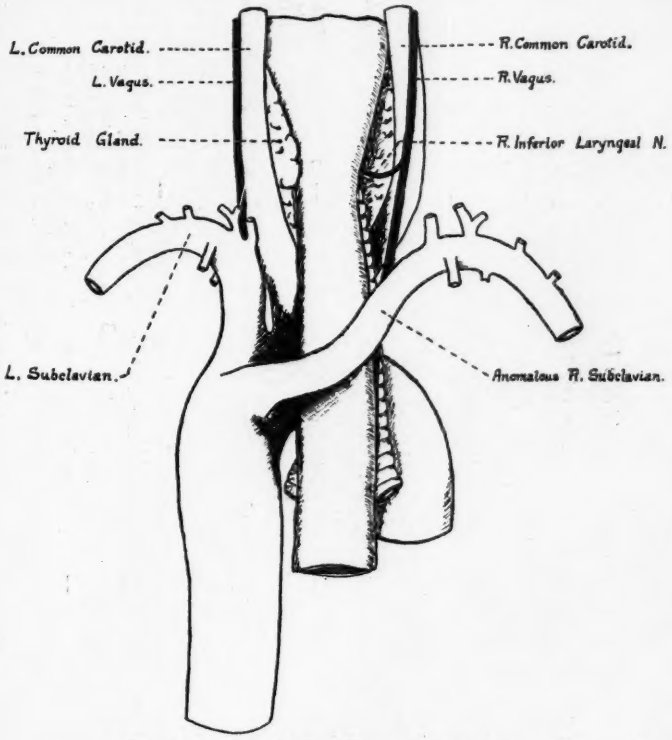

Fig. 1. Specimen in Case II, seen from behind.

assumption of an aortic-arch system composed of certain fixed segments, which, without the necessity of furnishing any adequate explanation of causes, may be obliterated or retained in any combination which suits the requirements of the case.

In a recent volume of *Contributions to Embryology*, E. D. Congdon (1922) presents the results of a detailed research in which he followed the successive changes in the aortic-arch system through a series of human embryos ranging from 1·3 mm. to 24 mm. in length, 29 stages being included in the series.

Table I

Year	Reported by	Subject	Branches of aortic arch	Origin of right subclavian	Course of right subclavian	Branches of subclavian	Origin of vertebral	R. inferior laryngeal nerve	Termination of thoracic duct
1871	Bradley	Female	—	Extreme left of transverse arch on posterior aspect	Between trachea and oesophagus	—	—	—	—
1888	Brodie	—	Bicarotid L. vertebral L. subclavian R. subclavian	—	Behind oesophagus	—	Right from R. common carotid. Left from aorta	—	—
1889	Shepherd	Female aet. 30	R. common carotid L. common carotid L. vertebral L. subclavian R. subclavian	Posterior part of aortic arch opposite 3rd thoracic vertebra	Behind oesophagus	—	Right from R. common carotid. Left from aorta	Turned round right vertebral	—
1892	Abbott	—	Bicarotid L. vertebral L. subclavian R. subclavian	—	Behind oesophagus	—	Right from R. common carotid. Left from aorta	—	—
1893	Clarkson	—	—	Posterior aspect of descending part of arch ½-inch below origin of left subclavian	—	—	—	Not recurrent	—
1897	Turner	Negro	—	Last branch of arch	Behind oesophagus	—	—	—	—
1909	Gould	Male	R. common carotid L. common carotid L. subclavian R. subclavian	Just beyond left subclavian opposite lower border of 3rd thoracic vertebra	Behind oesophagus, on bodies of upper 3rd thoracic vertebrae	From 1st part: vertebral, thyroid axis, internal mammary, superior intercostal. From 2nd part: none. From 3rd part: posterior scapular	Usual	Slight recurrency	Usual
1911	Geddes	—	—	—	Behind oesophagus	On R. side, first branch is superior intercostal proper On L. side, first branch is costocervical	—	—	—
1914	Cobey	Male negro aet. 45	R. common carotid L. common carotid L. subclavian R. subclavian	Dorsal aspect of descending limb of arch, ½-inch distal to left subclavian	Behind oesophagus, obliquely at an angle of 45 degrees	From 1st part: vertebral, transverse cervical. At junction of 1st and 2nd parts: inferior thyroid, suprascapular, internal mammary	Usual	Not recurrent	

1915	Gladstone and Wakeley	Male aet. 71	R. common carotid L. common carotid L. subclavian R. subclavian	Posterior aspect of arch at level of 4th thoracic vertebra	Behind oesophagus	On R. side:—From 1st part: vertebral, costo-cervical, inferior thyroid, common trunk of supra-scapular transverse cervical and internal mammary. From 2nd part: none. From 3rd part: Posterior scapular On L. side: vertebral, internal mammary, thyroid axis, superior intercostal, posterior scapular	Usual	Turned round inferior thyroid artery	Right angulus venosus
		Female aet. 63	Bicarotid L. subclavian R. subclavian	Posterior aspect of arch ½-inch beyond origin of left subclavian	Behind oesophagus	On R. side: vertebral, costo-cervical, thyro-cervical, internal mammary On L. side: vertebral, superior intercostal, internal mammary, inferior thyroid, transverse cervical, suprascapular	Usual	Turned round inferior thyroid artery	Usual
1915	Bevier	Caucasian female aet. 40 or 45	—	1 cm. distal to left subclavian	Behind oesophagus Related to 2nd thoracic vertebra, on which it produced a groove on left side and a flattening on ventral surface	On R. side: vertebral, deep cervical, ascending cervical, internal mammary, transversalis colli On L. side: vertebral, superior intercostal, ascending cervical, internal mammary, deep cervical, transversalis colli	Usual	Not recurrent	—
1917	Harvey	White male aet. 60	Bicarotid L. subclavian R. subclavian	Right side of descending arch at its commencement	Behind oesophagus, across body of 3rd thoracic vertebra. Considerably dilated up to the point where it emerges behind oesophagus	—	—	Represented by 3 or 4 twigs direct to larynx	Usual
		White male old age	Similar	—	Similar but not dilated	—	—	—	—
1921	Hudson	Male middle age	Bicarotid L. subclavian R. subclavian	Right side of descending arch at level of 3rd thoracic vertebra	Behind oesophagus, across 2nd and 3rd thoracic vertebrae. Presents a slight fusiform dilatation where it lies behind oesophagus	From 1st part: vertebral, internal mammary, thyro-cervical trunk, superior intercostal and deep cervical. From 2nd part: none. From 3rd part: posterior scapular	Usual	Round upper branch of inferior thyroid artery	Usual
1923	De Garis	Male negro	R. common carotid L. common carotid L. subclavian R. subclavian	Deep left extremity of aortic arch opposite 3rd thoracic vertebra	Behind oesophagus, crossing dorsal thoracic wall at an angle of 50 degrees to the horizontal	—	Right from R. common carotid. Left from L. Subclavian	Passed to larynx beneath inferior thyroid artery	—

He points out that these vessels do not in any complete sense recapitulate their phylogenetic history, and stresses the importance of recognising the formative influence of one developing organ on another. From the study of Congdon's paper, certain facts and principles become evident and throw new light on the theories which have previously been advanced regarding the anomalous subclavian artery. It therefore seems appropriate to refer briefly to these points at the present stage.

In tracing the development of the aortic-arch system, Congdon recognises two distinct phases:—(A) the branchial phase, in which the vessels approximate to the branchial pattern of lower vertebrates; (B) the post-branchial phase, during which the branchial pattern is being replaced by the adult arterial arrangement. Though it is not intended that the points mentioned here should represent anything approaching a complete summary of Congdon's paper, it is deemed advisable, for clearness, to arrange the remarks under the headings of these two phases.

A. *The Branchial Phase*

The branchial phase is regarded as commencing with the establishment of the first arch and as terminating with the interruption of the right pulmonary arch. It thus lasts about 22 days, viz. from the 23rd day of development (estimated average length of embryo 1·3 mm.) to the 45th day of development (estimated average length 12 mm.).

Due to the caudal movement of the heart relative to the pharynx, the aortic arches develop in regular order from cephalic to caudal; as the more caudal ones become developed, the first and then the second undergo involution. Thus, during the branchial phase, the blood-stream from the heart to the dorsal aorta on each side makes use of the following channels in succession: (*a*) first arch; (*b*) first and second arches; (*c*) second and third arches (*d*) third and fourth arches; (*e*) third, fourth and pulmonary arches, with in some cases the so-called fifth arch as well. The chief cause of the disappearance of the first and second arches is to be found in the transference of the blood-stream to the more caudal arches, as a result of the "descent" of the heart.

The last nine days of the branchial phase, represented by embryos from 6 to 12 mm. in length, constitute a period of relative stability of the aortic-arch system, termed the "late branchial period," during which the blood-stream from the heart to the dorsal aorta on each side is divided between the third, fourth, and pulmonary arches. By the end of the late branchial period these arches have, in association with the "descent" of the heart, moved as far caudally as the pharyngeal pouches and other structures allow. At the commencement of the late branchial period (fig. 2), the third, fourth, and pulmonary arches on each side radiate from a saccular enlargement, flattened dorso-ventrally, and situated cephalic to the truncus arteriosus. Before the end of the late branchial period, this enlargement has become completely separated into two parts (fig. 3): (*a*) a tubular pulmonary portion, from which

the pulmonary arches arise; and (*b*) a saccular aortic portion, termed the "aortic sac," from which the third and fourth arches arise. It is worthy of note that no ventral aortae occur in the human embryo; the external carotid, we may observe in passing, is therefore not formed from a vessel known as the ventral aorta, but is first seen as an independent sprout extending cephalically from the saccular enlargement referred to above; its origin is gradually displaced laterally to such an extent, that, at the end of the branchial period, it is seen to arise from the third arch at its junction with the aortic sac.

At the commencement of the branchial phase, the dorsal aortae are separated from each other along their whole length by the neural tube, the notochord, and the alimentary canal. Gradually, however, the neural tube becomes separated from the notochord by an interval (occupied by mesenchyme), in which, in the thoracic region, the dorsal aortae approach each

Fig. 2

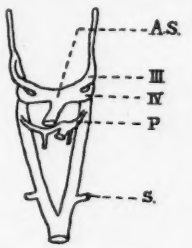

Fig. 3

Figs. 2 and 3. Aortic-arch system of the late branchial period (Congdon). III=third arch; IV=fourth arch; P.=pulmonary arch; A.S.=aortic sac; S.=primitive subclavian. Fig. 2 represents condition at the commencement, fig. 3 towards the end, of the late branchial period.

other until they lie almost in contact. Fusion of the dorsal aortae now occurs, commencing in the more caudal parts and gradually extending in a cephalic direction, actual fusion at any point being preceded by the development of transverse anastomoses. Such fusion is seen in progress in embryos of 3 to 6 mm.; the process thus comes to an end at the commencement of the late branchial period, by which time the cephalic end of the unpaired aorta, referred to as the "bifurcation," is opposite, approximately, the seventh body segment.

The primitive subclavian artery can first be recognised in embryos of 4 to 6 mm. (i.e. at the stage when the fourth arches are present but the pulmonary arches are not yet complete), when it takes the form of a slender channel lying in an intersegmental space and arising from an outpocketing of the aorta which also gives off a dorsal segmental artery. Soon this outpocketing from the aorta develops into the stem of a segmental artery, typically the seventh, of which the subclavian comes to be a branch. As the subclavian increases in size, it gradually incorporates the stem of the segmental

artery, which thus by the end of the branchial period has completely lost its identity in the subclavian; on the right side at least the subclavian is still referred to as the primitive subclavian. In Congdon's series, the primitive subclavian, or more correctly the stem of the segmental artery from which it arose, was found in all cases to arise at first from the unpaired aorta a short distance caudal to the bifurcation. As the aorta descends, however, the subclavian appears to be retained in position by its large vertebral branch, and thus its origin is gradually displaced in a cephalic direction on the aorta. In three out of four embryos of the late branchial period the origin of the subclavian was found by Congdon to be already from the paired aorta a little cephalic to the bifurcation (fig. 3).

The development of the vertebral by the formation of anastomoses between the first seven segmental arteries together with the interruption of the proximal segments of the first six is of course well recognised. Suffice it to state here that these processes commence in the latter part of the branchial period (two successive stages being shown by two 9 mm. embryos in Congdon's series), but are not complete until early in the post-branchial phase, when the vertebral is seen as a large vessel arising from the proximal part of the primitive subclavian.

B. *The Post-branchial Phase*

The post-branchial phase commences with the interruption of the right pulmonary arch (estimated average length of embryo 12 mm., 45th day of development); the essential changes of the phase are completed within two weeks, i.e. by the time the length of the embryo has reached 24 mm. It is worthy of note that a 24 mm. embryo has large arteries in the cephalic part of the body which differ only in minor details from those of the adult.

Of the various features of the post-branchial phase, only three will be mentioned here, viz.: (1) the interruption of the branchial pattern; (2) the migration of the origins of the innominate and left subclavian arteries; (3) the evolution of the right subclavian artery.

1. *The interruption of the branchial pattern.*

Early in the post-branchial phase the way is made clear for the evolution of the arch of the aorta and the great vessels arising from it by the interruption of the branchial pattern in the following situations, and in the order mentioned: (*a*) the right pulmonary arch distal to the origin of the right pulmonary artery; (*b*) the paired aorta on each side, between the third and fourth arches; (*c*) the right paired aorta caudal to the origin of the primitive subclavian. The time occupied by each of these interruptions is approximately one day; the last of them is well towards completion at the 16 mm. stage.

These interruptions are shown to have the following features in common.

(*a*) ***In all cases, the primary factor in the causation of the disappearance o the particular segment is a decrease in blood-flow leading up to an absence of blood-flow.*** In the case of the distal segment of the right pulmonary arch,

diminution in current is due to the fact that the left pulmonary arch represents a shorter and more direct route to the dorsal aorta than the right, and this in turn is due to the fact that the bifurcation which cuts off the pulmonary trunk is well to the left of the mid-sagittal plane (fig. 3); in this way the right pulmonary arch comes eventually to carry a supply of blood sufficient only for the right pulmonary artery, and in consequence the segment of the arch distal to the origin of the right pulmonary artery ceases to function. In the case of the dorsal aorta between the third and fourth arches, the interruption is preceded by the development of continuous curvature of the third arch with the part of the dorsal aorta cephalic to it and of the fourth arch with the part of the dorsal aorta caudal to it (fig. 4), such curves indicating that the current from the third arch is now passing cephalically while that from the fourth arch is passing caudally; as a consequence, the blood-flow in the segment of the dorsal aorta between the third and fourth arches comes to a standstill. In the case of the terminal segment of the right dorsal aorta, the diminution in blood-flow is due to the fact that the aortic trunk has now assumed an oblique direction, in accordance with which a greater proportion of blood passes viâ the left fourth arch and left paired aorta than viâ the right fourth arch and right paired aorta, which thus come eventually to retain a current adequate only for the supply of the right primitive subclavian; thus the current ceases in the segment of the right paired aorta distal to the origin of the primitive subclavian. As a result of the diminution in blood-flow, the wall of the vessel in each case becomes thickened and the lumen becomes diminished.

It would appear to be established that, when once any particular segment of the aorta-arch system ceases to function in the carrying of a portion of the blood-stream, that segment is destined to disappear; and that, on the contrary, as long as any particular segment continues to function in the carrying of a portion of the blood-stream, that segment does not undergo degeneration from any other cause. As an example of the latter principle may be mentioned the case of the left pulmonary arch, which, though exposed to pressure from the left vagus and its inferior laryngeal branch, so far from disappearing, actually increases in diameter at a time when the distal segment of the right pulmonary arch is in process of obliteration.

(*b*) *In all cases, a secondary factor exists in the form of tension thrown on the particular segment as a result of the "descent" of the aorta.* Tension appears to exert its influence only after the walls of the vessel have already become weakened; it then has the effect of stretching the weakened segment, thus leading to its interruption and favouring its disappearance.

(*c*) *In all cases, the disappearance of the interrupted segment is complete.* At a slightly later stage no trace of such segments can be found. Degeneration of a vessel into a fibrous cord, such as is seen in early extra-uterine life, does not occur at this early embryonic stage.

It is worthy of note that, in the case of the segment of the right dorsal

aorta distal to the origin of the primitive subclavian, the current descriptions and diagrams are incorrect in that they represent the obliteration as involving a long segment of the paired aorta. As a matter of fact, at a stage immediately preceding this interruption (fig. 5), the origin of the primitive subclavian is only a short distance cephalic to the bifurcation of the unpaired aorta; the portion of the right dorsal aorta which disappears is thus only an extremely small terminal segment.

2. *The migration of the origins of the innominate and left subclavian arteries.*

At the 14 mm. stage (fig. 5), the arch of the aorta and certain of the great vessels are seen to be roughly outlined. The aortic sac, lying cephalic to the aortic trunk, is seen to have differentiated into two limbs, right and left, of which the right is a more or less transverse tube, while the left is shorter and of greater diameter; from the lateral extremity of each limb arise the third

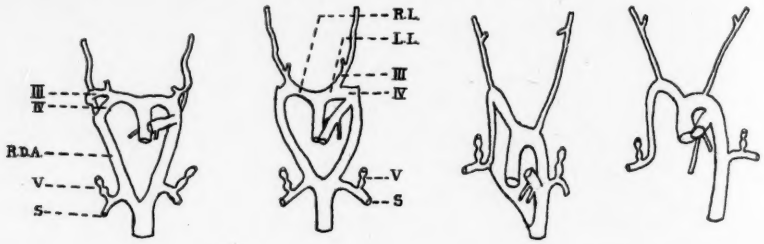

Fig. 4 Fig. 5 Fig. 6 Fig. 7

Figs. 4 to 7. Aortic-arch system of the post-branchial phase (Congdon). III = third arch; IV = fourth arch; R.D.A. = right dorsal aorta; R.L. = right limb of aortic sac; L.L. = left limb of aortic sac; V. = vertebral; S. = primitive subclavian. Fig. 4. 13 mm. embryo. Right pulmonary arch interrupted. Fig. 5. 14 mm. embryo. Dorsal aorta interrupted between third and fourth arches. Fig. 6. 16 mm. embryo. Right dorsal aorta caudal to primitive subclavian stretched to a thread. Fig. 7. 18 mm. embryo. Adult vessels recognisable.

and fourth arches. The arch of the aorta can be seen to be formed of the following parts, which are as yet distinguishable one from the other on account of irregularities and inequalities: (*a*) aortic trunk, (*b*) left limb of aortic sac, (*c*) left fourth arch, (*d*) left dorsal aorta. The innominate artery is represented by the right limb of the aortic sac. The origin of the external carotid has now moved laterally and cephalically for some distance along the third arch; thus the proximal segment of the third arch (as far as the origin of the external carotid) represents the common carotid, arising on the right side from the innominate and on the left side from the arch of the aorta. The primitive subclavian arises on each side from the dorsal aorta just cephalic to the bifurcation; the vertebral is complete and is a branch of the subclavian.

At this stage, the summit of the arch of the aorta is formed by the left fourth arch, and the left common carotid arises proximal to the summit. Due to more rapid growth of the segment of the arch of the aorta proximal to the

origin of the left common carotid relatively to the distal segment, the region of the origin of the left common carotid becomes later the summit of the arch.

Due to a totally different process, the origins of the innominate and left subclavian approach the origin of the left common carotid. This is due to a plastic rearrangement; "the substance of the wall is shifted about" to permit the movement of the origins. This process occurs while the heart is descending into the thorax, and no doubt takes place in response to tension thrown on the innominate and left subclavian. By the 24 mm. stage, the innominate has moved up alongside the left common carotid, while the origin of the left subclavian has passed the ductus arteriosus but is still separated from the origin of the left common carotid by an interval; at the 31 mm. stage, however, the left subclavian is shown lying close to the left common carotid.

A similar migration of the origin of vessels has been found in the large abdominal arteries. Evans (1912) suggests that such movements may be due to unequal growth of the ventral and dorsal walls of the main vessel. According to Congdon, the exact nature of the translocation of material appears to be at present very uncertain.

3. *The evolution of the right subclavian artery.*

When once the right dorsal aorta has become interrupted caudal to the origin of the primitive subclavian artery, any further movement of the origin of the latter vessel cephalically on the dorsal aorta becomes unnecessary. At this stage (fig. 7), the various developmental parts of the definitive subclavian can be recognised, viz.: (*a*) right fourth arch, (*b*) adjacent uninterrupted segment of right dorsal aorta, (*c*) primitive subclavian, which has already incorporated the stem of the seventh segmental artery.

By the time that the heart has sunk into the thorax and the sternal bands have fused, the curves of the right subclavian have disappeared and its developmental parts have become indistinguishable, the right fourth arch and adjacent part of the right dorsal aorta having lost their identity in the subclavian. In this way a channel of considerable tortuosity has become relatively straight at a time when the embryo as a whole has increased only about 30 per cent. in length; such a change in the subclavian must obviously have been produced by a great slowing in the rate of growth in length of its wall.

The developmental explanation of the usual type of anomalous right subclavian passing dorsal to the oesophagus

A. *The generally accepted view*

The generally accepted theory of the occurrence of the anomalous right subclavian is to the effect that it arises by a failure of the caudal segment of the right dorsal aorta to become interrupted, this segment becoming incorporated in the right subclavian as its proximal part in lieu of the right fourth arch and the segment of the right dorsal aorta adjacent to it. The position of the anomalous subclavian dorsal to the oesophagus favours the interpre-

tation that the distal part of the right dorsal aorta is included in the abnormal artery, while the uniform failure of the inferior laryngeal nerve to be recurrent round it certainly indicates that it includes no portion of the right fourth arch.

In elaborating this theory in the light of Congdon's findings, we may, for the sake of convenience, confine our attention at this stage to those cases in which the right vertebral arises in the usual manner from the subclavian. Cases in which the right vertebral arises from the right common carotid will be referred to separately in discussing the course of the right inferior laryngeal nerve.

We have already seen that the evolution of the normal subclavian is permitted by the interruption of the segment of the right dorsal aorta distal to the origin of the primitive subclavian, and that, just previous to this interruption (fig. 8 A), the primitive subclavian takes origin from the right dorsal aorta only a very short distance cephalic to the bifurcation of the unpaired aorta. The occasional occurrence of an anomalous subclavian would

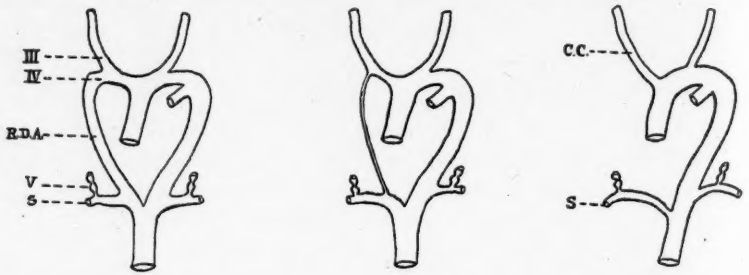

Fig. 8. To illustrate the generally accepted theory of the formation of an anomalous right subclavian artery of which the vertebral is a branch. III=third arch; IV=fourth arch; R.D.A.=right dorsal aorta; C.C.=common carotid; V.=vertebral; S.=subclavian.

appear to be due in all probability to the primitive subclavian tapping the main blood-stream in the unpaired aorta by means of the short terminal segment of the right dorsal aorta, and in this way receiving its blood-flow by the shorter route. When we consider the proximity of the origin of the primitive subclavian to the unpaired aorta, it is not surprising that this should occasionally occur. Under such circumstances, the caudal segment of the right dorsal aorta, having acquired a new function in conveying a portion of the blood-stream, is not subject to the influence of a factor which would ordinarily have caused its disappearance. For a short time, no doubt, the cephalic segment of the right dorsal aorta also continues to carry blood to the primitive subclavian; it seems likely, however, that the caudal segment, when once the blood-flow through it towards the primitive subclavian is definitely established, proves the more advantageous route. In response to the greater demand thus thrown on the blood-stream in the unpaired aorta, the proportion of the current passing to the unpaired aorta viâ the left dorsal aorta probably in-

creases, with the result that the right limb of the aortic sac comes eventually to carry a proportion only of the current adequate for the supply of the right common carotid. Thus the right fourth arch and the cephalic part of the right dorsal aorta come to be an area of diminishing blood-flow (fig. 8 B), and, ceasing to function, become interrupted (fig. 8 C) in accordance with the general principle seen in the interruption of certain portions of the branchial pattern.

This interruption, though possibly occurring a little later than the time at which the caudal segment of the right dorsal aorta usually becomes obliterated, no doubt occurs at a relatively early stage, and therefore we should expect the disappearance of the segment to be complete. The earlier interruption of the right pulmonary arch caused the inferior laryngeal branch of the right vagus to come into relation with the right fourth arch, while the disappearance of the latter leaves no structure derived from the original branchial pattern round which the nerve should pass. Contrary to the opinion expressed by Gould (1909), one would not expect to find any fibrous cord representing the degenerated fourth arch, since at this early stage degeneration of a vessel to a fibrous cord does not occur.

The anomalous subclavian, at the time of its formation (fig. 8 C), takes origin from the developing aorta at a point corresponding to the bifurcation of the unpaired aorta and therefore distal to the origin of the left subclavian. The fact that in the adult the origin of the anomalous vessel is commonly found at a considerably higher level is no doubt due to the migration of its origin in a cephalic direction during the descent of the aorta into the thorax. The anomalous subclavian is obviously exposed to the same influences as the normal innominate and left subclavian, and no doubt the movement of its origin occurs by the same process as is responsible for the movement of these vessels.

B. *Gould's theory of the vessels by which the terminal segment of the right dorsal aorta is normally represented*

Gould (1909), in affirming the generally accepted theory of the origin of the anomalous subclavian by the incorporation of the caudal segment of the right dorsal aorta, raised the question of the vessels by which, if any, the caudal segment of the right dorsal aorta is represented in the ordinary case where a normal right subclavian is present.

At this time, apparently, the view that the right superior intercostal artery represented a portion of the caudal segment of the right dorsal aorta was fairly generally accepted, and a further portion of this segment was assumed to exist in the form of either a vas aberrans from the aorta or an anastomosis between the superior intercostal and the first aortic intercostal; as a necessary adjunct to this theory, it was further assumed that the anomalous subclavian when it occurred, incorporated a portion of the right superior intercostal. It was against the view that the right superior intercostal represents any portion of the right dorsal aorta that much of Gould's

argument was directed. Whatever criticism has been and may still be brought against any part of his reasoning, it is I think generally recognised to-day that his conclusion was entirely correct. It now appears to be definitely established that the longitudinal stem of the superior intercostal artery on both sides arises by a process similar to that which occurs in the development of the vertebral, i.e. by the establishment of anastomoses between certain segmental arteries and the disappearance of their proximal segments.

Gould, however, in rejecting the theory of the superior intercostal as a portion of the right dorsal aorta, expressed his opinion in favour of another theory, to the effect that the caudal segment of the right dorsal aorta is frequently if not normally represented by a vas aberrans from the right subclavian and a second vas aberrans either from the aorta or from the first aortic intercostal; these vessels he appears to have regarded as fairly constant in their occurrence, for he deprecates the omission of the first of them from certain of the standard text-books.

This theory in its turn was criticised by Gladstone and Wakeley (1915), who found, from the examination of a series of embryos over 17 mm. in length, that in every case the terminal segment of the right dorsal aorta had completely disappeared. This observation harmonises with the more recent finding of Congdon, whose figures of reconstructions clearly show that normally the disappearance of this segment is absolute. Gladstone and Wakeley further pointed out that, in 16 subjects in which they specially looked for the aberrant branch of the subclavian, they were able to find no trace of it, from which they concluded that, whatever the frequency of this branch, it is certainly not normally present.

From the references which I have located there appears to be nothing to indicate any considerable frequency in the occurrence of this aberrant branch. The following extracts may be taken as typical of the descriptions usually given. Poirier and Nicolas (in Poirier and Charpy's *Traité d'anatomie humaine*, 1912) refer to it as follows: "Un vaisseau aberrant qui descend derrière l'artère vertébrale et l'oesophage, et se termine dans les parois de l'aorte thoracique. Ce rameau est intéressant au point de vue morphologique, car il représente la racine droite descendante de l'aorte thoracique." Thane (in Quain's *Elements of Anatomy*, 1892) describes it as "a small vessel arising from the right subclavian artery near the vertebral, and descending to the left between the oesophagus and spine to join the termination of the arch; it is a vestige of the right aortic root. A brach arising in this situation and terminating on the trachea and oesophagus is not uncommon." Shepherd (1889), in another section of the paper in which he describes his case of anomalous subclavian, mentions an instance of a branch from the first part of the right subclavian passing down behind the aortic arch to reach the bifurcation of the trachea; he further says: "I have several times seen this artery. On one occasion it reached the descending aorta, with which it communicated, and I looked upon it as a persistence of the right aortic root."

From these descriptions, there would appear to be two types of aberrant branch occasionally seen arising near the commencement of the right subclavian; the one passing to the trachea or to the trachea and oesophagus; the other passing behind the oesophagus to reach the arch of the aorta, with which it may communicate.

It is evident that the first type of vas aberrans does not represent any part of the right dorsal aorta. Whether the second type does represent the normally interrupted terminal segment of the right dorsal aorta appears to be undetermined. The position and form of such an aberrant vessel are certainly suggestive of a stretched and attenuated but unobliterated terminal segment of the right dorsal aorta. The observations of Gladstone and Wakeley and more recently of Congdon show definitely that normally in the human embryo this segment has completely disappeared after the 17 mm. stage. This however cannot be taken as proving that the segment cannot occasionally be represented in the adult by a vas aberrans, for if it be admitted that the segment may sometimes persist as a portion of the right subclavian, then it is but reasonable to admit that it might also occasionally persist in another form. From developmental considerations it does not appear to be impossible that the vas aberrans might arise in this manner, provided for some reason the blood-flow in the terminal segment of the right dorsal aorta does not cease at the usual stage. For example, it may happen that, owing to delay in the production of sufficient inclination of the arotic trunk to the left, the right dorsal aorta, at a time when its terminal segment should disappear, continues to carry a little more blood than is adequate for the supply of the primitive subclavian, the excess continuing to pass by way of the terminal segment of the right dorsal aorta to the unpaired aorta. Under such circumstances one would expect the lumen of this terminal segment to become diminished in accordance with its diminished blood-flow, while, what little current there is, is likely to prevent complete obliteration. Meanwhile the larger cephalic segment of the right dorsal aorta has begun to be incorporated in the definitive subclavian in the usual manner. It seems possible that, with the continued descent of the developing aorta, the already dwindling and possibly weakened caudal segment may become stretched without of necessity becoming obliterated throughout, and in this way giving rise to a vas aberrans occupying approximately the position of the "thread" shown in fig. 6.

On the contrary, however, the case described by Geddes (1911 *a*) shows, in addition to an anomalous right subclavian, an unusual anastomosis between the right superior intercostal and a vas aberrans which arises from the aorta by a trunk common to it and the first left aortic intercostal. In position and form this vessel closely resembles the type of vas aberrans just referred to, from which it differs mainly in the fact that it is connected with the superior intercostal instead of directly with the subclavian. It is evident that the small vessel described by Geddes cannot represent the terminal segment

of the right dorsal aorta (since the latter is incorporated in the anomalous subclavian), but must be of entirely separate origin. And if this vessel could arise quite independently of the right dorsal aorta, then it seems probable that the occasional vas aberrans previously referred to might similarly be, from a developmental point of view, a structure entirely independent of the right dorsal aorta.

To what extent, then, Gould's hypothesis is correct remains undetermined. It may or may not be that the vas aberrans passing from the subclavian to the aortic arch, in those rather rare cases when it occurs, represents the terminal segment of the right dorsal aorta. Gould's view that this aberrant branch is almost constant in its occurrence appears, however, to be clearly disproved.

C. *Geddes's theory of two types of anomalous right subclavian*

Geddes (1911 *a*), while accepting Gould's conclusion that the right superior intercostal is developmentally a structure entirely separate from the terminal part of the right dorsal aorta, reasoned from the specimen already referred to that two types of anomalous right subclavian probably occur. Type 1, in which the obliteration of the whole right dorsal aorta is complete, and the anomalous subclavian is produced by the opening up of a channel of anastomosis between the first aortic intercostal and the right superior intercostal. Type 2, in which the anomalous subclavian is produced, according to the usual theory, by incorporating the distal segment of the right dorsal aorta, while the proximal segment, which usually becomes a part of the subclavian, disappears.

Regarding the possibility of the occurrence of an anomalous subclavian of Geddes's first type, it must be admitted that, provided it be granted that in some cases the whole of the right dorsal aorta may become obliterated, then an efficient right subclavian would probably be produced in the manner suggested by Geddes. The aspect of this theory, however, which requires further scrutiny is the question of the probability of the whole of the right dorsal aorta ever becoming obliterated from any cause. Viewed from the developmental standpoint, such an obliteration certainly seems improbable. From the study of the normal changes which occur in the aortic-arch system, it is evident that no portion of the system ever becomes obliterated except in response to the primary factor of a decrease in blood-flow, and further, that, provided any portion of the system continues to function in carrying a part of the blood-stream, that portion cannot become obliterated from any other cause. It therefore seems reasonable to assume that the right dorsal aorta as a whole could not become obliterated unless some other more advantageously placed channel had already deprived it of its share of the current. Since, according to Geddes's theory, the channel which forms the proximal segment of the anomalous subclavian is the anastomosis between the first aortic intercostal and the right superior intercostal,

one is no doubt justified in concluding that this anastomosis would be the vessel concerned in diverting the blood-stream from the right dorsal aorta. It is certainly difficult to conceive any case in which such a channel would prove a more advantageous route from the unpaired aorta to the primitive subclavian than that offered by the terminal segment of the right dorsal aorta.

The only case in the literature at my disposal in which it is suggested that the anomalous subclavian may be of Geddes's first type is the case recorded by De Garis (1923), who describes the right subclavian as being "both relatively and absolutely small throughout, its size suggesting type 1 of Geddes." From the diagram one would judge the diameter of the vessel to be about two-thirds that of the common carotid and not quite two-thirds that of the left subclavian. The relatively small diameter of this vessel does not appear to be adequate proof of its formation by the opening up of a channel of anastomosis; and, in view of the objections from the developmental standpoint, one believes that it cannot be regarded as established that cases ever occur in the manner indicated by Geddes's first type.

D. *The value of adult branches as evidence of the mode of formation of the anomalous subclavian*

In the papers of Gould (1909), Geddes (1911 *a*), and Gladstone and Wakeley (1915), considerable prominence is given to the position of origin, form, and anastomotic branches of the superior intercostal artery as evidence for or against the views under discussion. Indeed Gould, in his opening remarks, refers to the records of previous cases as affording "no information on the details of the condition such as the branches which the artery gives off, on the study of which the true interpretation of the abnormality depends."

In the light of more recent investigations on the development of arteries, it seems reasonable to doubt whether arguments based on the observation of the branches in the adult are of the value which has been attributed to them. Woollard (1922), from his study of the development of the forelimb arteries in the pig, concludes that in the formation of an individual arterial tube three stages may be distinguished: (1) the stage of the capillary net; (2) the stage characterised by enlarged tubes showing island-formation, coalescence, and a tendency to fuse—the retiform stage; (3) the stage of the formation of a definite stem; each of these stages occurs in response to definite physiological demands. In the human embryo, at the relatively early stage when the terminal segment of the right dorsal aorta becomes interrupted, it is evident that the branches of the subclavian have by no means assumed their adult form. If, then, at this early stage, an abnormal subclavian should commence to be evolved in place of a normal subclavian (either in the manner suggested by the usual theory or in any other way), then it is but reasonable to suggest that the branches of the subclavian, being as yet incompletely formed and relatively "plastic," may later in response to physiological

demands assume a form which in the adult will merely conform to one of the recognised types. For example, in the case of a subclavian being formed (if that be possible) by the opening up of a channel of anastomosis according to the theory of Geddes's first type, it appears to be possible that the superior intercostal might still in the course of subsequent development assume the form which is regarded as normal in the adult, instead of giving any indication of the mode of formation of the anomalous parent trunk. Again the presence in the adult of an anastomosis between the superior intercostal and the first aortic intercostal cannot be regarded as a conclusive argument that the abnormal subclavian has not arisen at an early stage by the opening up of such a channel of anastomosis unless we are in a position definitely to assert the impossibility of a second anastomosis occurring between these two arteries.

Further, in considering the evolution of adult branches, the phenomenon of migration of branches along the trunk of the parent vessel must be borne in mind. Thus it is possible that the position of the origin of the superior intercostal relative to that of the vertebral may be different in the adult form from what it was at the stage when the subclavian first became outlined.

In view of such considerations, one believes that a reasonable degree of caution should be exercised before accepting as conclusive, arguments which, being based on the study of adult branches, imply that the form and position of such branches are already immutable at the time when the definitive parent trunk commences to be outlined.

The course of the right inferior laryngeal nerve in cases of anomalous right subclavian artery

Reference to Table I shows that, in cases of anomalous right subclavian artery, the right inferior laryngeal nerve may present one of three courses: (1) it may be recurrent round the right vertebral artery; (2) it may turn round the inferior thyroid artery or one of its branches; or (3) it may pass to the larynx directly.

1. *Cases in which the nerve is recurrent round the right vertebral artery*

Although the table of cases given in this paper contains only one definite instance (viz. the case of Shepherd, 1889) in which the nerve turns round the vertebral artery, the perusal of the literature leads me to believe that not only have similar cases been recorded but that also in all such cases the origin of the right vertebral is from the right common carotid. Thane (Quain's *Elements of Anatomy*, 1892) states that, in all cases of anomalous right subclavian in which the right vertebral arises from the right common carotid, the inferior laryngeal nerve passes inwards to the larynx around the first part of the vertebral artery.

The occurrence of a right vertebral arising from the right common carotid and having the inferior laryngeal nerve recurrent round it has been explained on the very reasonable assumption that the vertebral in these cases has in-

corporated part or the whole of the right fourth arch together with, possibly, the adjoining part of the right dorsal aorta.

On the point, however, of how the vertebral comes to incorporate these parts of the original branchial pattern, the existing statements are far from clear. According to Shepherd (1889), the condition is explained by the disappearance of the fourth arch external to the origin of the vertebral. Thane (in Quain's *Elements of Anatomy*, 1892) offers the following explanation: "The subclavian is derived from the dorsal aorta while the vertebral is continued from the fourth arch, the connection of the latter with the dorsal aorta being obliterated." Cobey (1914), in explaining the anomalous subclavian as due to absorption of the fourth arch, states that the extent and position of the absorption appear to determine the point of origin of the vertebral; if the absorption is not complete medially, then the unabsorbed portion persists as the vertebral arising from the common carotid. Goldbloom (1922) states that obstruction medial to the origin of the vertebral at an early period results in the vertebral arising from the anomalous subclavian, while obstruction beyond the origin of the vertebral results in the vertebral arising from the common carotid. Apart from the fact that these statements all imply the dropping out of certain fixed segments of the branchial pattern from no apparent cause, they are further open to objection in that they are completely lacking in significance unless we assume the origin of the primitive vertebral to be either from the right dorsal aorta or from the right fourth arch, independent of and cephalic to the primitive subclavian. In an arterial arrangement such as depicted in fig. 5, no disappearance of any portion of the fourth arch (Shepherd), or obliteration of the connection of the fourth arch with the dorsal aorta (Thane), or failure of absorption in the medial part (Cobey), or obstruction anywhere along the fourth arch and right dorsal aorta (Goldbloom), could possibly result in the origin of the vertebral from the common carotid.

It is therefore evident that, in order to explain the occurrence of an adult right vertebral which arises from the common carotid and in which the right fourth arch is incorporated, we must assume that, prior to the interruption of the right dorsal aorta, the primitive vertebral arose from the right dorsal aorta cephalic to the origin of the primitive subclavian, as indicated in fig. 9 A.

In this connection it is interesting to note that, in three out of four cases in the table in which the right vertebral is definitely stated to arise from the right common carotid, the left vertebral is also unusual in that it arises from the arch of the aorta proximal to the origin of the left subclavian. In these cases, then, not only did the right vertebral at a relatively early stage arise from the right dorsal aorta proximal to the primitive subclavian, but also at some stage the left vertebral arose from the left dorsal aorta in a corresponding position.

In seeking an explanation as to why one or both vertebrals should arise from the paired aortae in this manner, three possible theories suggest them-

selves. At first sight it seems possible that the origin of the vertebral may have migrated medially from the subclavian on to the paired aorta. On closer inspection, however, factors to cause such a migration appear to be entirely lacking. On the contrary, in the case of a normal subclavian the much more medial position of the origin of the right vertebral in the adult as compared with its position when the right subclavian is first outlined (fig. 5) appears to be explained entirely by a relative failure of growth of the part of such a subclavian derived from the right fourth arch and the right dorsal aorta. The second theory which suggests itself is that the proximal portion of the primitive subclavian may have become absorbed into the paired aorta, a theory which has been used by Robinson (in Cunningham's *Text-book of Anatomy*, 1922) to explain the origin of the left vertebral from the arch or the aorta, and also by Harris (1922) to explain the origin of the left vertebral from the left dorsal aorta in a case of an entirely different nature. On the left side, where the paired aorta undergoes a considerable increase in diameter, such an absorption appears to be by no means impossible, but even here the theory is open to objection in that there appears to be no reason why such an absorption should occur in a few cases and not in all. In the case of the right side, where the diameter of the paired aorta is becoming diminished, the theory appears to be quite untenable. The third and simplest theory seems to be the most probable, namely that in such cases the vertebral has from its inception incorporated the stem of the sixth segmental, while the subclavian has incorporated the stem of the seventh segmental in the usual manner. In favour of this theory is the fact that independent origins of the primitive vertebral and of the primitive subclavian on the right side would confer a tendency towards the development of an abnormal rather than a normal subclavian; while the fact that in some cases the primitive vertebral may at an early stage arise from the paired aorta cephalic to the primitive subclavian is clearly demonstrated by the aortic-arch system of the 17 mm. stage described by Gladstone and Wakeley (1915). In this case the left vertebral had an independent origin from the left dorsal aorta about midway between the left common carotid and the left subclavian.

Assuming, then, a case in which, at say the 14 mm. stage, the primitive vertebral and the primitive subclavian are seen to arise independently from the right dorsal aorta (fig. 9 A), we may construct the history of the subsequent changes very briefly as follows. The right paired aorta is as yet uninterrupted at any point caudal to the fourth arch, but, owing to the inclination of the aortic trunk to the left, the right fourth arch and right paired aorta are now carrying a much smaller proportion of the blood-stream than the corresponding parts on the left side. The diminishing current in the right paired aorta is being mainly taken by the primitive vertebral, in consequence of which the primitive subclavian, deprived of a sufficient blood-flow by the usual route, comes to tap the main stream in the unpaired aorta by means of the short terminal segment of the right dorsal aorta (fig. 9 B). Thus, in

the short segment of the right dorsal aorta between the origin of the primitive vertebral and the origin of the primitive subclavian, the current becomes greatly diminished, eventually ceases, and as a result the segment itself disappears. In this way the permanent vessels come to be outlined (fig. 9 c), the vertebral now consisting of the right fourth arch, the adjacent uninterrupted part of the right dorsal aorta, and the primitive vertebral, while the subclavian consists of the short caudal segment of the right dorsal aorta together with the primitive subclavian.

Should a similar arrangement of the primitive vertebral and primitive subclavian exist on the left side (fig. 9), though a segment of paired aorta intervenes between their origins, this segment, since it continues to function

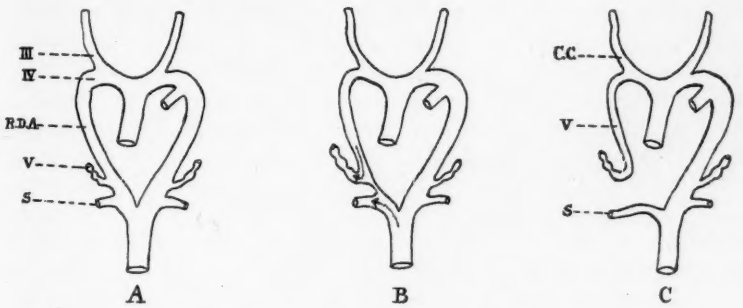

Fig. 9. To illustrate the theory of the formation of an anomalous right subclavian artery with the vertebral as a branch of the right common carotid. III=third arch; IV=fourth arch; R.D.A.=right dorsal aorta; C.C.=common carotid; V.=vertebral; S.=subclavian.

in the conveyance of the main blood-stream, shows no tendency towards interruption but develops in the usual manner into a portion of the definitive aorta. During the descent of the aorta, the origin of the vertebral no doubt migrates in a cephalic direction in the same manner as the origin of the left subclavian, so that in the adult it arises from the summit of the arch between the left common carotid and the left subclavian.

The recent case recorded by De Garis (1923) differs from those already referred to in hat, while the right vertebral arises from the right common carotid, only that portion of the inferior laryngeal nerve which is distributed to the trachea and oesophagus is recurrent round it; the rest of the nerve passes to the larynx beneath the inferior thyroid artery. In the absence of any detailed account of the early development of the inferior laryngeal nerve, one is led to assume that in this case only a portion of the nerve was ever caudal to the right fourth arch, the remaining filaments being cephalic to it from the beginning. Such a possibility is suggested by Hudson (1921) for the whole nerve; "it seems probable that here the cervical visceral branches of the vagus came off above the fourth aortic arch instead of below it, and in

consequence were not drawn down the neck in a loop during the caudal migration of the heart and great vessels."

2. *Cases in which the nerve is recurrent round the inferior thyroid artery or one of its branches*

In those cases in which the nerve does not pass round the vertebral artery it may be assumed that the disappearance of the right fourth arch and the cephalic segment of the right dorsal aorta has been complete. The varying relation of the nerve, in such cases, to the inferior thyroid artery is no doubt explainable on the basis of the normal variation of the relation of the artery to that part of the nerve which is in relation with the thyroid gland; it is a well-established fact that the artery may pass entirely behind or entirely in front of the nerve, or that some of the branches of the artery may pass in front of and some behind the nerve. Cases in which, in the presence of an anomalous subclavian, the nerve loops round the whole of the inferior thyroid artery no doubt represent cases in which, had the fourth arch persisted, the nerve would, when in the region of the thyroid gland, have passed entirely behind the artery; cases in which the nerve loops round one or more of the upper branches of the artery no doubt represent cases where the nerve would have had some of the branches of the artery in front of it and some behind it; while cases in which the nerve bears no relation to the artery no doubt represent cases where the nerve would have passed entirely in front of the artery.

3. *Cases in which the nerve passes direct to the larynx*

In those cases in which the nerve is recurrent round neither the vertebral nor the inferior thyroid artery, it is usually described as passing directly to the larynx.

Gould (1909), however, pointed out that, in his case, the nerve did not take the shortest possible course from the vagus to the lower border of the inferior constrictor, but presented a slight curve with the convexity downwards. A similar condition existed in the second of the cases which I have seen.

Gould suggested that such recurrency is a question of the point in development at which the permanent arterial pattern becomes defined, and expressed the opinion that further cases would (in the absence of any structure round which the nerve turned) show varying degrees of recurrency, being greater in cases where there is more delay in the outlining of the permanent arterial pattern. Up to the present, however, the prophecy contained in the latter part of this statement remains unfulfilled. From the consideration of the normal arterial development and the theories based upon it, it would seem that, although individual cases may show some very slight variation in the time at which the anomalous subclavian is outlined, it is improbable that there is any considerable variation in this point. It is quite possible that Gould's theory represents the correct explanation of the difference between a perfectly straight and a slightly curved course such as has been

observed, yet it appears unlikely that there is sufficient variation in the time of interruption of the right dorsal aorta to account for any marked variation in the degree of recurrency of the nerve.

THE QUESTION OF THE OCCURRENCE OF AN ANOMALOUS RIGHT SUBCLAVIAN PASSING EITHER IN FRONT OF THE TRACHEA OR BETWEEN THE TRACHEA AND THE OESOPHAGUS

In the series of approximately 200 cases collected by Holzapfel in 1899, the anomalous subclavian, though described in the majority of cases as passing behind the oesophagus, was stated to pass between the trachea and oesophagus in 20 cases, and in front of the trachea in six cases. More recently, however, Geddes (1911 *b*) has expressed doubt as to whether any definitely substantiated case exists in which the artery occupied either of the latter two positions.

With regard to the course of the artery ventral to the trachea, Geddes found, on investigating the literature, that references to such a position of the artery appeared to rest for their authority on the case recorded by Walter in 1785, which Geddes believes to be a "case of right aortic-arch with the right subclavian artery arising last and representing the left arch, and so passing in front of the trachea." It is interesting to note that the observation of Walter was also doubted by Quain (1844).

With regard to the course of the anomalous subclavian between the trachea and oesophagus, Quain (1844) appears to accept as genuine the cases of Bayford and of Meckel, while Geddes appears to regard both of these as at least doubtful. Concerning Meckel's observations, Geddes is disposed to the opinion that Meckel had not seen a case. As the quotations given by Quain and by Geddes differ, it may not be out of place to mention the passage quoted by Quain: "Dem normalen näher ist der Weg zwischen der Luft und Speiseröhre, welchen diese Arterie bisweile nimmt. Dies fand in dem dritten der von mir beobachteten Fälle" (*Handbuch der Pathol. Anatomie*, Band 2, S. 100).

In the opening paragraph of Geddes's paper, there occurs a statement to the effect that the description of the anomalous subclavian as passing either between the trachea and oesophagus or in front of the trachea appears to rest on the authority of Power. In view of the fact that Geddes's conclusions have been accepted without question by certain more recent writers, it is unfortunate that this statement, on which the remainder of his paper is based, is not entirely correct, since it leaves out of account the very definite case recorded by Bradley (1871). The anomalous artery in this case (observed in the dissecting-room of the Manchester School of Medicine and Surgery) is described as follows: "It sprang from the extreme left of the transverse arch on its posterior aspect, and passed upwards and to the right, running between the oesophagus and trachea to continue down the arm in the usual manner." The position of this vessel with relation to the trachea and oesophagus is

emphasised in a footnote, in which Bradley refers to a second case of anomalous right subclavian observed during the same session. in the second case, the artery "did not, as in the former instance, pass between the trachea and oesophagus, but behind them both."

It must therefore be admitted that at least one definite case has occurred in which the anomalous right subclavian artery passed between the trachea (ventrally) and the oesophagus (dorsally). The developmental explanation of such a position of the vessel is by no means obvious. One can but suggest that, in this case, the fusion of the paired aortae to form the unpaired aorta may have occurred, at any rate in its cephalic part, ventral to the alimentary canal instead of dorsal to it; and that subsequently the anomalous artery was developed by the incorporation of the terminal segment of the right dorsal aorta in the usual manner.

The branches of the anomalous right subclavian artery

The suggestion of Gould (already referred to) that it is on the study of the branches of the abnormal subclavian that the true interpretation of the anomaly depends appears to have resulted in the recording, by practically all the more recent writers on this subject, of the branches of one or both subclavian arteries in the cases observed by them.

Although it is not impossible that such records of branches may later prove to be of value, they do not appear, in the writer's opinion, to have thrown any particular light on the causation of the anomaly. Indeed, in consideration of the investigations recorded by Thomson (1893) and De Garis (1924) on the branching of the normal subclavian artery, it would seem that the branches of the anomalous artery, though showing considerable variation, are no more variable in their origin than the branches of the normal artery.

The termination of the thoracic duct in cases of anomalous right subclavian artery

Geddes (1911 *b*) states that "another legend which haunts this arteria variation is that the thoracic duct ends usually on the right side." According to Geddes, this statement appears to rest on the condition found in one case in the middle of the eighteenth century, and described in the Museum Anatomicum of Sandifort.

Of the cases recorded since the appearance of Geddes's paper, one of the two cases reported by Gladstone and Wakeley (1915) showed the thoracic duct terminating at the junction of the right internal jugular and subclavian veins; while in a case reported in 1916 by Poynter (quoted by Hudson) the thoracic duct divided opposite the fifth thoracic vertebra into two trunks, of which the larger opened into the right, and the smaller into the left, angulus venosus. Reference to Table I shows that, of five cases in which the termination of the thoracic duct is definitely stated, in four the duct terminates in

the usual manner on the left side; this was also the case in the two instances which I have seen. From the few cases mentioned, it appears obvious that the duct terminates usually on the left side and less frequently on the right.

That the thoracic duct is not always of the type described in the text-books is clearly shown by Davis (1915), who points out that seven distinct types of thoracic duct have been observed, while from developmental considerations two further types probably exist. Though the cases given by this observer appear to be too few to justify the use of percentages, it is evident from his paper that in the majority of cases the thoracic duct terminates on the left side as usually described, while a smaller number of cases definitely exists in which the duct either terminates on the right side or divides to terminate on both sides.

In connection with the anomalous subclavian, neither from the records of cases nor from theoretical considerations does there seem to be any indication that the termination of the thoracic duct on the right side is more frequent in such cases than would be expected from the normal variations of the duct itself.

Clinical significance of the anomalous right subclavian artery

From the frequency with which the anomalous right subclavian has been observed in dissecting-room subjects, it must I think be obvious that the majority of such cases occur without the production of any symptoms during life. From the clinical point of view, various possibilities have been suggested by some of the writers on this subject; of such suggestions, a few appear to be substantiated by definite cases, while many appear to be merely in the nature of surmise.

The possibility of unequal radial pulses is mentioned by Harvey (1917) and Goldbloom (1922). The same writers also mention that, in at least one recorded case, the unusual position of the artery caused difficulty in the operation for ligation of the subclavian. Harvey further suggests that in surgical conditions involving the oesophagus and in operations on the thorax the presence of the anomalous artery may be of considerable importance, while Goldbloom directs attention to the unusual position of the inferior laryngeal nerve in connection with operations on the front of the neck. Cobey (1914) suggests the possibility of symptoms similar to those of cervical rib. Goldbloom (1922) mentions the possibility of pressure on the thoracic duct, in which connection it is interesting to note that, in the case recorded by De Garis (1923), the thoracic duct was more than usually varicose, and in addition presented a definite dilatation for about 4 cm. just before passing beneath the anomalous subclavian.

The possibility of dysphagia being caused by an anomalous subclavian has been referred to by a number of writers dating back at least to Bayford, whose case was described in 1794. The earliest reference to this question in the literature at my disposal appears in the writings of Quain (1844) who gives

some particulars of Bayford's case. A female who died at the age of nearly 62 had occasional difficulty in swallowing from childhood; the condition became worse at puberty, and thereafter was aggravated once or twice a month throughout life; for three weeks before death the patient was scarcely able to swallow; post-mortem, nothing could be found to which the difficulty in swallowing could be assigned except the presence of the right subclavian between the trachea and the oesophagus, from which it was "reasonably concluded that the vessel was the source of the symptoms." Quain refers to this case as "an isolated observation which has not been confirmed"; he points out that in the majority of cases there is no dysphagia, and cites the case of Otto, in which a young man who was observed for some time before death had not had the slightest difficulty in swallowing, but was found post-mortem to have an anomalous subclavian artery between the oesophagus and the vertebral column. More recently it has been suggested by Holzapfel (quoted by Harvey) that only by an aneurismal enlargement of the abnormal subclavian may dysphagia be produced. In the cases recorded in the present century, dilatation of the part of the vessel related to the oesophagus is stated by Harvey to have been observed in one of the cases collected by Bean in 1904, and in the table of cases in this paper is shown to have occurred in one of the two cases recorded by Harvey (1917) and in the case recorded by Hudson (1921).

Summary and Conclusions

1. The anomalous right subclavian artery arising from the arch of the aorta distal to the origin of the left subclavian appears to be not uncommon. At least 231 cases have been recorded, and two further cases are presented here. The frequency with which the condition has been observed by different writers varies from 4 in 1000 to 4 in 225.

2. Reference is made to the recent research of Congdon on the developmental changes in the aortic-arch system in the human embryo, from the study of which it appears evident that the classical descriptions of this portion of embryology as they appear in most of our standard text-books require revision. In view of certain facts and principles brought out by Congdon, it has appeared advisable to review the existing theories and discussion on the anomalous subclavian artery, since such statements have hitherto been based on the incomplete and in some respects inaccurate data provided by the description and diagrams of Rathke.

3. The occasional occurrence of an anomalous right subclavian artery appears to be adequately explained on the assumption that the primitive subclavian in such cases taps the main blood-stream in the unpaired aorta by means of the short terminal segment of the right dorsal aorta; this segment thus escapes its usual fate of disappearance consequent upon an absence of function, and becomes incorporated in the definitive subclavian. The suggestion of Geddes that in some instances the anomalous subclavian arises by

the opening up of a channel of anastomosis between the first aortic intercostal and the right superior intercostal appears to be very improbable from developmental considerations and is not substantiated by actual cases.

4. Congdon's work, as well as the earlier observations of Gladstone and Wakeley, shows that as a general rule in normal cases the short segment of the right dorsal aorta distal to the origin of the primitive subclavian disappears altogether. That no portion of this segment is represented in the normal right superior intercostal is definitely proved, but whether the segment may occasionally be represented by an aberrant branch from the right subclavian appears uncertain.

5. In view of the fact that the branches of the subclavian are, at the time when the anomalous parent vessel is no doubt outlined, as yet incompletely formed and later may be modified considerably in response to physiological demands, it is suggested that reasonable caution should be exercised in the examination of arguments which are based entirely on the position of origin, form, and anastomoses of the branches as seen in the adult.

6. The right inferior laryngeal nerve in cases of anomalous subclavian is found, by reference to the literature, to take one of three courses to the larynx. Firstly, it may be recurrent round the right vertebral artery, which in such cases arises from the right common carotid; in these cases it appears evident that the vertebral has incorporated the right fourth arch and an adjacent portion of the dorsal aorta. It is suggested that the factor which is mainly responsible for the development of such an arterial pattern consists probably in the primitive vertebral having incorporated the stem of the sixth segmental artery and having failed to establish the usual anastomosis with the seventh segmental artery. Secondly, the nerve may turn round the inferior thyroid artery or one of its branches; or, thirdly, the nerve may pass direct to the larynx. In all such cases the right fourth arch has no doubt disappeared completely (degeneration of a vessel into a fibrous cord does not occur at this early stage). The varying relation of the nerve to the inferior thyroid artery appears to be nothing more than the expression in such cases of the normal variation of the relation of the nerve to the artery (and its branches) in the region of the thyroid gland.

7. That the anomalous subclavian artery passes in the great majority of cases dorsal to the oesophagus is of course established. Whether such a vessel ever passes ventral to the trachea or between the trachea and oesophagus has been doubted. The observations of Quain and more recently of Geddes indicate that there is no reliable case in which the artery is shown to pass in front of the trachea. In the matter of the passage of the artery between the trachea and the oesophagus, the case of Bayford may be open to doubt, but the case of Bradley constitutes one definitely recorded instance of an extremely rare condition.

8. The branches of the anomalous right subclavian appear to be no more variable than the branches of the normal subclavian, and the thoracic duct

in such cases appears to show only its normal variation in form and termination.

9. Undoubtedly the great majority of cases of anomalous subclavian artery produce no symptoms and pass unrecognised throughout life. In the matter of clinical significance, different writers have suggested various possibilities, a number of which appear as yet to be purely hypothetical.

II. TWO CASES OF AN UNUSUAL RELATION OF THE INNOMINATE ARTERY TO THE TRACHEA

Cases in which the innominate artery lies ventral to the cervical portion of the trachea consist as a rule of the condition known as "high bifurcation" of the innominate; in such instances the vessel ascends in front of the trachea, with a gradual inclination to the right, and terminates at a higher level than usual.

Two cases of a rather different nature from this well-recognised type have recently come under my notice, having been observed in the dissecting-room

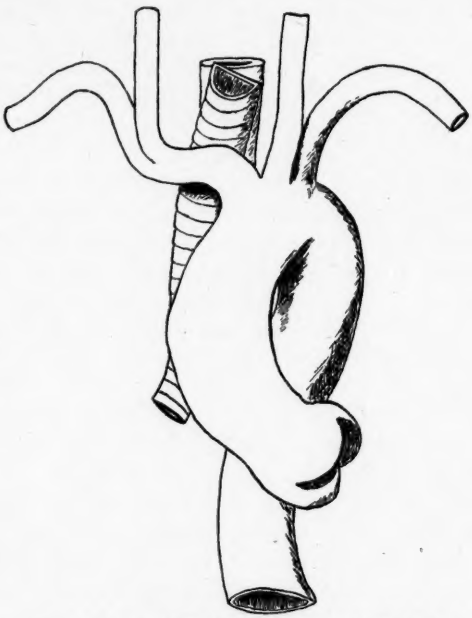

Fig. 10. Specimen from first case, seen from front.

on successive days. In both cases the innominate artery was seen in the dissection of the neck to pass transversely in front of the trachea at about the level of the suprasternal notch, and on further investigation I found the main features of the condition to be as follows.

In the first case (fig. 10), the summit of the arch of the aorta was at the level of the suprasternal notch, and from it the innominate artery arose at what appeared to be the usual point. From its origin the innominate artery passed to the right, being at first inclined slightly upwards but for the most part lying horizontally. It lay ventral to the trachea, on which it produced a definite impression, and terminated in the usual position behind the right sterno-clavicular joint. The length of the vessel was about 1¼ inches.

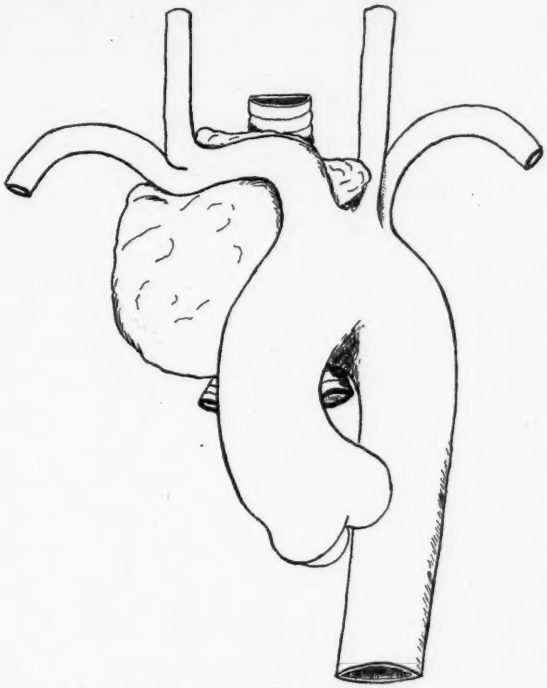

Fig. 11. Specimen from second case, seen from front.

Only the upper part of it was visible above the suprasternal notch, and here it was partly overlapped by the thyroid gland, which was enlarged. The thoracic portion of the vertebral column showed definite scoliosis, the convexity being directed towards the right. Apparently as a result of this condition, the trachea, at the point where the innominate artery crossed it, was disposed to the right of its normal position. The heart was normal in size and in its position relative to the ventral thoracic wall. The aortic orifice occupied its usual position behind the lower border of the third left costal cartilage at its junction with the sternum; the aortic arch was not atheromatous or dilated. The subject was a male aged 81, and the cause of death was certified as cerebral haemorrhage.

In the second case (fig. 11), the summit of the arch of the aorta was again at the level of the suprasternal notch. The innominate artery, arising at apparently the usual point on the arch, first ascended for about ¾ inch, and then passed transversely to the right to terminate a short distance above and lateral to the right sterno-clavicular joint. Its total length was about 2 inches. In its ascending portion and at the commencement of its transverse portion it lay ventral to the trachea, from which it was separated by a part of the mass of tissue shown in the figure. This mass lay in the superior mediastinum mainly to the right of the trachea, but was partly placed between the trachea behind and the transverse part of the arch of the aorta and the innominate artery in front. A small portion extended to the left between the origins of the innominate and left common carotid arteries. The innominate artery occupied a groove in it, being separated by less than ¼ inch from the trachea. The mass was definitely encapsulated, and on histological examination was found to consist entirely of fat. Practically the whole width of the transverse portion of the innominate artery was visible above the suprasternal notch, and was separated by an interval from the thyroid gland, which was small and atrophic. The heart was enlarged and hypertrophied, the arch of the aorta was atheromatous and dilated, and the innominate artery was also dilated near its origin. The subject was a male negro aged 72, and death was certified as due to myocarditis and heart failure.

The only instances of a similar condition which I have been able to find mentioned in the literature consist in two cases recorded by Koster and described in English by Moore (1867). In one of these cases the innominate artery, arising "just under the jugular notch of the sternum," ran for nearly 3 cm. above the sternum directly in front of the trachea and then turned to the right before dividing into its two branches. The subject was a female aged 75. "The arch of the aorta lay high, was atheromatous and ossified, dilated about one-half more than in the normal state." In the other case the course of the innominate was similar, but the portion of the vessel which ascended ventral to the trachea and above the sternum was only 1¾ cm. in length; the subject was a male aged 40. Koster points out that the condition does not appear to have been previously described; he regards it as a "congenital abnormal position of the arteries."

In the two cases which I have seen, it is not impossible that the position of the innominate artery may be explained as resulting from the pathological changes shown to be present. In the first case, it is obvious that the occurrence of scoliosis has caused the supero-inferior extent of the left half of the thorax to become diminished. As a consequence of this, the arch of the aorta may have become raised relatively to the skeleton of the thorax, while the innominate artery, subjected to pressure from above by the enlarged thyroid gland, may have been caused to assume a more or less transverse position. In the second case it is possible that the obvious dilatation of the arch of the aorta is the factor which accounts for the high position of the

summit of the arch, while the course of the innominate artery may be accounted for by the height of the arch, and the dilatation of the commencement of the innominate itself, together. The presence of the fatty mass (in which the artery was embedded) was a possible factor which prevented the vessel from becoming still further elevated into the neck.

In the first case at least I am disposed to doubt the accuracy of such a theory. Examination of the specimen shows that the aorta appears to have accommodated itself to the diminished vertical extent of the left half of the thorax by the development of a marked curve in its descending thoracic portion following the abnormal curve of the vertebral column, rather than by elevation of the arch. The aortic valves occupied their usual position relative to the ventral thoracic wall, the ascending portion of the arch appeared to be normal in its course and direction, while the innominate artery with the other two large vessels arose in the usual manner from the region of the summit of the arch. It thus appeared that the relatively high position of the summit of the arch was accompanied by an increase in the length of that segment of the arch which extends from the aortic valves to the origin of the innominate, a condition which could not have been caused by pathological changes in the skeleton of the thorax.

It may therefore be permissible to point out as an alternative theory that the practically transverse position of the innominate artery may conceivably be due to arrest of the descent of the arch of the aorta at the stage when it reached the inlet of the thorax. At this stage, as has been shown by Congdon (1922), the innominate artery still takes the form of a transverse tube, and in the course of normal development only later becomes longitudinal in response to the caudal movement of the arch.

In conclusion, I desire to express my thanks to Prof. W. P. Gowland for permission to publish the cases which have occurred in the dissecting-room of this department.

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ROENTOLOGICAL INJECTION MASSES—OLD AND NEW

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The study of the course of blood-vessels, by injection into them of some opaque material and subsequent use of the Roentgen ray, has been in vogue since 1896 (1)—in fact, from the earliest days of X-ray work. Consequently, it is not surprising to find in the literature descriptions of many and varied masses, which have been elaborated from time to time, since that date; yet, when a piece of research work was commenced in 1921, on the study of the blood supply of muscle and the kidney, it was impossible to find, after many trials, a mass suitable for the purpose.

It was for this reason, then, and not from a mere vain desire to expand further an already distended literature, that the mass to be described here was elaborated.

A mass, to be of universal utility—for use in the adult cadaver, the foetus or the isolated organ—should possess the following properties:

(*a*) Perfect homogeneity—there must be no coarse granules which would block the finer vessels and consequently interfere with the completeness of the injection.

(*b*) It must be sufficiently thin in consistency to run into the finest arterioles.

(*c*) It should be miscible with formalin and other liquids: that is to say, that when the mass comes into contact with formalin or with blood or saline (used for washing out the contained blood) in the vessels of the cadaver or organ, there should be no "separation out" of the mass.

(*d*) The mass must "set" in the vessels after injection, to enable subsequent dissection to be undertaken, without oozing and staining of the tissues, or to allow sections of the organ, or part under consideration, to be cut.

(*e*) It must cast a clear, dense shadow with the X-rays.

(*f*) No heat must be required to introduce the mass into the vessels.

(*g*) It must permit of easy manipulation.

As stated above, the literature on this subject is extensive, despite statements to the contrary by H. C. Orrin (2), and in attempting to account for the inability to find a suitable mass, the following reasons may be advanced:

1. The varied purposes for which the masses were prepared—each author putting forward a slightly different mass for a slightly different object. An attempt has been made here to prepare a mass suited to all types of injections.

2. Many of these masses, recorded in the literature, were prepared for

zoological studies; these, in most instances, are not applicable to the study of the adult cadaver.

3. Methods of preparation are described without accompanying radiographs being shown.

4. Scantiness or absence of instructions as to the mode of preparation of the mass.

5. Great variation, in different countries, in the quality and nature of the chemical materials used. Thus, in the case of vermilion, workers in this field refer to the substance as plain vermilion, without specifying whether the English, Chinese or Austrian variety is intended for use—and yet this substance varies widely in its composition.

6. Methods have been described by authors as suitable and yielding good results—these same methods, used for the same purposes, only to be rejected by subsequent investigators as useless.

Measures have been adopted to eliminate the first five faults: over the last there is no control—my only hope is that no difficulty will be experienced with the mass described below, which has already been used by other investigators in this Anatomy Department with success.

Among the substances which have from time to time been used as bases for X-ray injection masses, we find

1. Barium salts (3, 4, 5).
2. Bismuth salts (6, 7, 8).
3. Lead salts (9, 10).
4. Metallic mercury (11, 12, 13) and mercury salts (14, 15).
5. Calcium salts (16).
6. Colloids (17).

The advantages of the particular metal or salt selected and the disadvantages of the other metals are widely proclaimed by each investigator and in reading these accounts it is sometimes difficult to correlate their statements.

After many trials, vermilion was selected; space will not permit entering into the reasons for this choice, but the chief difficulty experienced was in combining concentration of vermilion, non-separation of the mass, setting and maintenance of the required consistency.

Finally, the following mass was elaborated:

Pale English Vermilion	dr. 2.
Glycerin. Amyli (B.P.)	dr. 3.
Liniment. Terebinth (B.P.)	dr. $1\frac{1}{4}$.
Pulv. Tragacanth. Co. (B.P.)	gr. 1.
Pulv. Amyli (B.P.)	gr. 3.
Water	dr. $1\frac{1}{2}$.

To make 4 drachms of the mass, i.e. concentration of vermilion is 1 in 2.

Prepare in following fashion: Into a perfectly dry mortar, insert dr. 2 of the Pale English Vermilion, add dr. 3 of glycerine of starch, rub into a paste

with the pestle, being careful to remove all lumpiness. Add dr. $1\frac{1}{4}$ of turpentine liniment, slowly and triturating constantly.

Now add gr. 1 of Pulv. Trag. Co. very slowly (gr. $\frac{1}{10}$ per 15 secs.), in order that it may become intimately mixed with the mass. Subsequently, insert in the same manner gr. 3 Pulv. Amyli—great attention being paid to the careful addition of the tragacanth and starch. The mass is now ready to thin down, by adding slowly dr. $1\frac{1}{2}$ water, triturating thoroughly.

The mass thus prepared possesses the following properties:

(*a*) It is sufficiently thin to flow easily through a "test cannula." This cannula was used for injections of the foetal femoral artery, the internal bore at its narrowest part being 0·75 mm.

(*b*) It is homogeneous.

(*c*) It is easily prepared.

(*d*) It is miscible with water, formalin or blood—that is, no separation out of the constituents occurs when the mass comes into contact with these substances to the extent which might take place during an injection.

(*e*) It is "tacky" within 18 hours and a test-tube filled with the mass can be inverted in 18 hours, without any loss of the contents of the tube. Subsequently, the mass sets hard and sections of the organ or part may be cut.

(*f*) The concentration of vermilion is 1 part in 2.

(*g*) The soapy nature is conducive to a very free flow. During the course of injection of the renal artery, the mass has been seen entering vessels in the capsule, which were only visible with a hand lens.

(*h*) It is easy to manipulate.

(*i*) The cost is about 3*d.* per fluid ounce.

In connection with the material for injection, this should be as fresh as possible—the fresher the material, the better the injection. With regard to all material obtained for injection, the word "fresh" should be translated "unpreserved"; because a part, the subject of decomposition, as far as the limits of nasal endurance, is more suited to injection than preserved material. The stage of rigor mortis should be avoided—a specimen which is stiff may be improved by soaking in water for 24 hours.

As to the mode of injection, direct pressure with an all-metal syringe was found to give the best results, with the golden rule "Do not hurry it": it should take 4 hours to fill the renal artery of an adult kidney and the pressure should never rise above 130 mm. Hg.

One other point—do not leave the organ, part or cadaver in one position during injection; raise it off the bench or roll it from one side to the other. The resistance offered by the part in contact with the bench is sufficient to prevent the entry of the injection into that part. The precise method of dealing with the kidney will be detailed in a later communication on the application of this mass to a study of the blood supply of this organ.

Finally, it is useless, nay, even unwise, to attempt to dogmatise concerning the exposures necessary in radiographing a part—each radiographer knows

his own apparatus best. The great value of stereoscopic radiographs in enhancing the beauty of the specimens and facilitating their interpretation is so well established that it does not call for further comment.

The accompanying radiographs are reproduced to illustrate the variety of uses of the mass: further radiographs will be shown in two later communications on the blood supply of muscle and the kidney.

I desire to express my very best thanks to Professor J. S. B. Stopford for his unfailing kindness, and for his help and advice, the liberal giving of which has endeared him to so many.

DESCRIPTION OF PLATES

Fig. 1. The upper extremity of a foetus of 7 months to show the vessels injected from the thoracic aorta.

Fig. 2. To show the vessels supplying the posterior tibial nerve in an adult (prepared by Dr D. Ramage).

Fig. 3. An injected portion of small intestine of a foetus.

Fig. 4. Vessels of the gastrocnemius muscle partially injected to demonstrate larger branches only.

Fig. 5. Vessels of the gastrocnemius muscle to demonstrate the smaller branches.

Fig. 6. Oblique section of the kidney to demonstrate the hypo-vascular line of Hyrtl.

Fig. 7. Fine perforating arteries (at arrow points) seen emerging from surfaces of injected kidneys of foetus.

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Fig. 1

Fig. 3

Fig. 2

Fig. 4

Fig. 5

Fig. 6

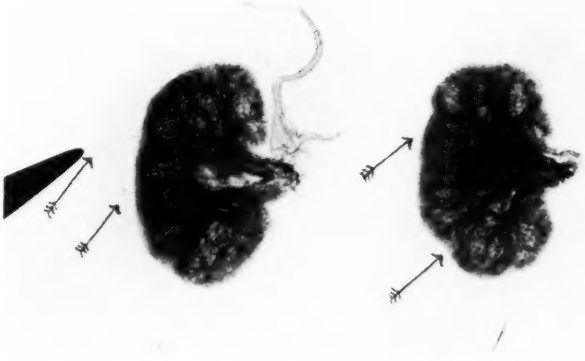

Fig. 7

THE DEVELOPMENT OF THE COLUMELLA AURIS IN THE CROCODILIA

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The development of the reptilian columella has been studied in considerable detail by a large number of workers, and, in most of the subclasses, is now well known. Nevertheless, in the copious literature which has grown up on this subject, relatively very few papers can be found which deal with the Crocodilia, and these often in a very inadequate manner. Since W. K. Parker's paper of 1881 there has been only one paper published (Shiino, 1914) which describes more than a few embryos, so that an investigation of the subject seemed desirable.

This work has been carried out in the Laboratory of the Anatomy School, Cambridge, during the tenure of a Frank Smart Studentship from Gonville and Caius College. I am indebted to Dr Hans Gadow, F.R.S., not only for the suggestion of the subject, but also for his interest and helpful criticism during the progress of the work, and for the loan of several specimens from his own collection and from the Zoology Museum. My thanks are due also to Professor Wilson, F.R.S., both for his criticism of the paper itself and for the advice he has given me, mainly with regard to technical methods. Finally, I must acknowledge the assistance I have received from Mr Walter Calcott in the preparation of sections and in the photography of the specimens and models.

The subject will be considered under the following heads:

1. Description of material and methods.
2. Description of individual embryos.
3. Connected account of the development of the columella.
4. General discussion.
5. Summary.

1. MATERIAL AND METHODS

The material consisted of eight embryos in all, three of which were crocodiles of uncertain species, but stated to be either *Crocodilus palustris* or *porosus*, and the remaining five, different stages of *Alligator mississipiensis*. The crocodiles will be referred to as Crocodile I, II, and III and the alligators in a similar way as Alligator I, II, etc., the numbers following one another in the order of the size of the embryos, the smallest coming first.

The crocodiles had the following dimensions:

	Greatest length (crown—rump)	Head length (snout—midbrain)
Crocodile I	1·3 cms.	·9 cm.
Crocodile II	1·4	·8
Crocodile III	1·6	·9

The embryos were cut in paraffin at 10 μ (except Crocodile III, which was cut at 12 μ) and were all stained with Delafield's haematoxylin and eosine, Crocodiles I and III in bulk, and Crocodile II on the slide. The bulk stain gave the better differentiation. The plane of section was horizontal to the head and parallel to the line of the mouth for Crocodile I, transverse to the head and perpendicular to the line of the mouth for Crocodile II, and sagittal for Crocodile III.

The dimensions of the alligators were:

	Greatest length (crown—rump)	Head length (snout—midbrain)
Alligator I	1·8 cms.	1·1 cms.
Alligator II	2·0	1·2
Alligator III	2·5	1·6

Alligators IV and V were of a very much later stage, and it was impossible to measure them in the same way. The body length was therefore determined as accurately as possible along the curvature of the animal from the snout to the end of the tail, and the head length along the line of the mouth. The results were as follows:

	Body length	Head length
Alligator IV	18·0 cms.	3·2 cms.
Alligator V	22·5	3·6

The first three alligators were treated in much the same way as the crocodiles.

Alligator I was cut into 10 μ sections, parallel to the line of the mouth and horizontal to the head, and stained with Delafield's haematoxylin and eosine on the slide.

Alligator III was treated in exactly the same way, except that the sections were 15 μ thick.

Alligator II was cut into 15 μ sections perpendicular to the line of the mouth, having been stained in bulk with Delafield's haematoxylin and eosine.

Alligator IV. The posterior part of the head only was embedded in celloidin, and cut into 30 μ transverse sections. Various stains were tried, but on the whole Delafield's haematoxylin and eosine were found to give the best results.

Alligator V was kept for dissection in order to serve as a guide in interpreting the sections of Alligator IV.

All the embryos had been photographed, so that it was possible to obtain an outline of the head for use in the graphical reconstruction of different parts. Crocodile II was photographed after it had been cleared in cedar-wood oil, so that an outline of the brain and less distinct indications of other structures were obtained. This was found of very considerable service in preparing graphical reconstructions. A wax-plate reconstruction was made of the columella and associated parts of Alligator II. All these reconstructions will be described in due course, and any further details with regard to the method used will be given then.

In size Crocodile II corresponds roughly with Parker's 1st Stage, but

actually it is rather later; the same applies to Crocodile I. Crocodile III is probably slightly earlier than Parker's 2nd Stage, while Alligators I and II are both slightly later. Alligator III is slightly earlier than Parker's 3rd Stage. Alligators IV and V lie between Parker's 6th and 7th Stages.

Voeltzkow (1899) has published an exhaustive account of the development of the external body form of *Crocodilus madagascariensis*. My Crocodiles I and II correspond fairly closely with his figure 57, Taf. VIII, and Crocodile III is rather more advanced, but not so much as figure 58, Taf. VIII. The alligators cannot be matched so easily against Voeltzkow's crocodiles, but Alligators I and II lie somewhere between figures 58 and 59, Taf. VIII, and Alligator III fairly close to figure 60, Taf. VIII.

There is one point of terminology which it would be well to settle before passing on to a description of individual embryos. The strand of cartilage which connects the extracolumella with the retroarticular part of Meckel's cartilage was homologised by Parker with the ceratohyal of lower groups. A homology of this strand with the dorsal part of the hyoid arch has been accepted by many writers (Huxley, Versluys, Shiino, etc.), but there is no reason for supposing that it is in any way homologous with a definite segment of the hyoid in the Ichthyopsida as the use of the term "ceratohyal" would suggest. On the other hand, this cartilaginous strand certainly does not correspond with the hyoid arch as a whole, so that as the term "ceratohyal" seems to be in common use, I shall adhere to it for descriptive purposes. For a similar reason I shall adhere to Parker's term "epihyal" for the nodule of cartilage sometimes found intervening between the upper end of the ceratohyal and the extra columella.

2. DESCRIPTION OF INDIVIDUAL EMBRYOS

Since the graphical reconstruction was made from Crocodile II (the photographs of this embryo being the most satisfactory), I shall describe it first. It is true that Crocodile I is slightly younger, but the difference is not important, and a previous description of the reconstruction will be of great help in understanding the condition of this embryo as well as that of the others.

Crocodile II

This embryo is characterised externally by a prominent beak-like snout, and a relatively short under jaw. The ventral ends of the second and third visceral arches are still plainly visible on the outside, although only the second cleft remains open. Internally, centres of chondrification have appeared in all the most important parts of the chondrocranium, and the process is well advanced in the mesethmoid, trabeculae, parachordals, and mandibular arch. The otic capsule, however, is still entirely blastemal.

The columella consists of two distinct divisions, medial and lateral. The medial division has an expanded medial extremity, the foot-plate, which presses into the blastema of the otic capsule. This foot-plate possesses a centre of chondrification (fig. 1, ***F.P.***) and is easily distinguishable from the otic

capsule. The lateral end of the medial division of the columella is in close contact with the lateral division, while dorsally it is continuous with a well-developed "processus dorsalis" (Versluys) or "suprastapedial" (Parker) (figs. 1 and 2, ***P.D.***). I shall adhere to Versluys' term. This processus dorsalis, seen in the reconstruction (fig. 2, ***P.D.***) possesses its own centre of chondrifica-

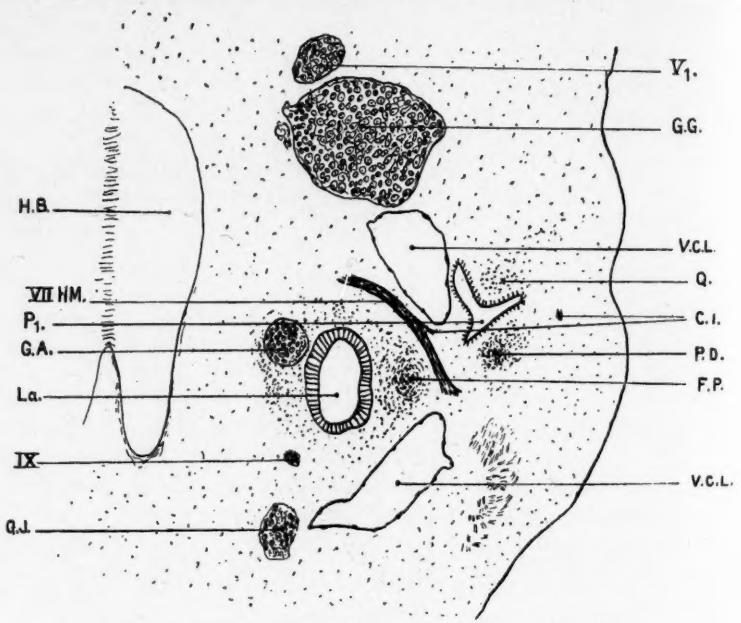

Fig. 1. Crocodile II. Horizontal section dorsal to columella.

A.C.I. arteria carotis interna; *A.S.C.* anterior semicircular canal; *A.T.O.* arteria temporo-orbitalis; *C.* columella; *C.H.* ceratohyal; *C.T.* chorda tympani; *E.C.* extracolumella; *E.C.M.* extracolumella muscle; *E.F.* ear-flap; *E.H.* epihyal; *E.St.* extrastapedial; *F.C.* fenestra cochleae; *F.P.* foot-plate; *F.V.* fenestra vestibuli; *G.A.* ganglion acusticum; *G.G.* Gasserian ganglion; *G.J.* jugular ganglion; *H.* hyoid cornu; *H.B.* hind brain; *I.St.* infrastapedial; *L.* Lateral division of columella; *La.* lagena; *L.S.C.* lateral semicircular canal; *M.* Meckel's cartilage; *O.C.* otic capsule; P_1. 1st pharyngeal pouch; P_2. 2nd pharyngeal pouch; $P_1.D.$ dorsal pocket of 1st pharyngeal pouch; $P_2.D.$ dorsal pocket of 2nd pharyngeal pouch; $P_1.R.$ ridge on 1st pharyngeal pouch between the quadrate and the ceratohyal; *P.D.* processus dorsalis; *P.S.C.* posterior semicircular canal; *Q.* quadrate; *R.Rec.* ramus recurrens ad trigeminum; *S.* stem of columella; *S.C.G.* superior cervical ganglion of the sympathetic system; *Tr.* trabecula; V_3. 3rd visceral arch; V_4. 4th visceral arch; *V.C.L.* vena capitis lateralis; V_1. ophthalmic division of *V*; V_2. maxillary division of *V*; V_3. mandibular division of *V*; *VII HM.* ramus hyomandibularis of *VII*; *VII Pal.* ramus palatinus of *VII*.

tion, and extends to a point close to the postero-dorsal angle (otic process) of the quadrate, from which, however, it is separated by the dorsal extremity of the 1st pharyngeal pouch (fig. 2, ***$P_1.D.$***). The otic process of the quadrate extends rather further in a dorsal direction as slightly condensed blastema

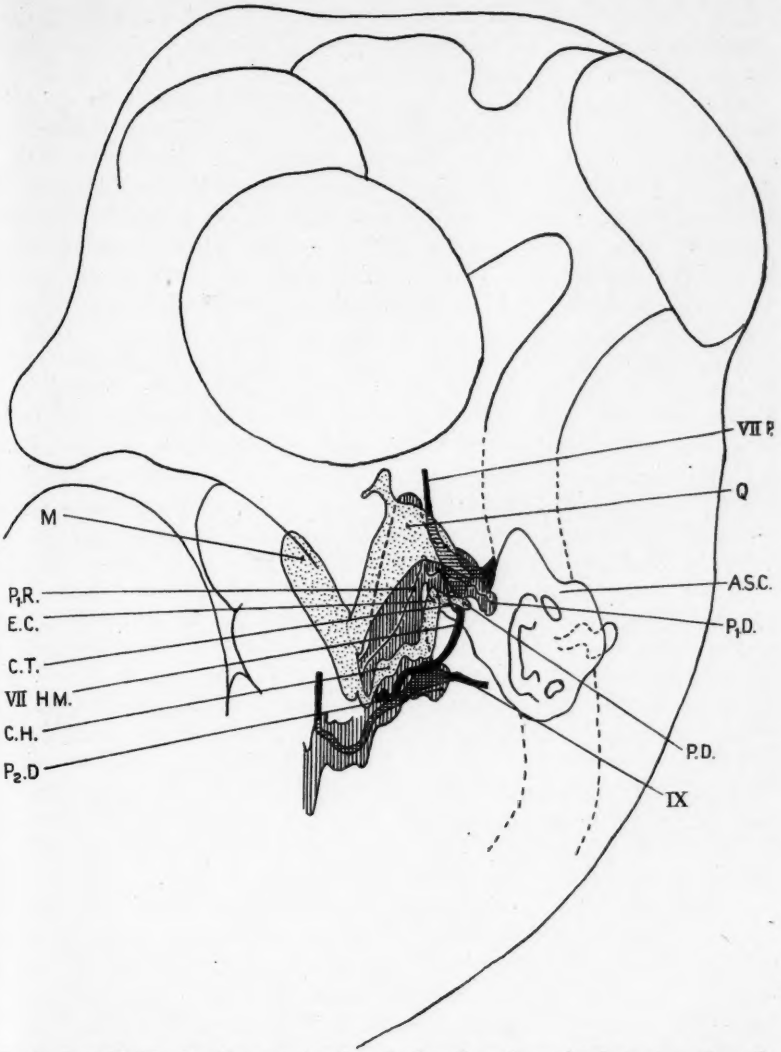

Fig. 2. Crocodile II. Graphic reconstruction of columella and associated structures from the lateral aspect.

Stippled areas—cartilage. Vertical lines—entoderm of 1st and 2nd pharyngeal pouches. Solid black or horizontal lines—nerves and ganglia.

than is shown in the reconstruction (fig. 2). The lateral division of the columella consists simply of a nodule of embryonic cartilage, considerably elongated in a caudal direction. The centre of chondrification is recognisable, but not so clearly as the two centres in the medial division. Its general shape in lateral

view can be seen from the reconstruction (fig. 2, *E.C.*). This caudal elongation is probably the beginning of an "infrastapedial" process, which will be described in later embryos.

The ceratohyal (fig. 2, *C.H.*) is a kinked strand of procartilage which is continuous above with the caudal end of the lateral division of the columella. It can be distinguished from the columella because of the circular disposition of its cells. There is no separate epihyal to be found. Ventrally it fades off into very slightly condensed blastema which is apparently continuous with the retroarticular part of Meckel's cartilage, as is shown in the reconstruction. This point was a little difficult to determine, mainly on account of the sparseness of the blastema in this region. The plane of section, too, was not convenient.

Little need be said about the quadrate and Meckel's cartilage. The general position and shape of these two elements can be seen quite clearly in the reconstruction (fig. 2, *Q*, *M.*). They are both well chondrified, although their outlines are still a little indistinct. This applies particularly to the quadrate.

The basi-lingual cartilage is a plate-like mass of procartilage, lying just below the larynx. Its cranial border, which is markedly convex, lies just cranial to the level of the quadrato-mandibular articulation. Immediately caudal to this level there are traces of blastemal processes from the sides of the plate which may represent the ventral ends of the hyoid arches. They are difficult to make out in this embryo because of the plane of section, and are far better shown in Crocodile I (fig. 4, *H.*). They are quite unconnected with any other skeletal element. A little further caudally well-developed 3rd visceral arches are found; they curve laterally round the pharynx, behind the 2nd pharyngeal pouch and slightly medial and anterior to the IXth nerve. Still further caudally the median body of the hyoid is continued as paired blastemal processes lying on either side of the trachea and slightly ventral to it. These probably represent the 4th visceral arches. A graphical reconstruction has been made of the body of the hyoid and its appendages in Crocodile I (fig. 4), and would serve almost equally well for this embryo.

The 1st visceral pouch is large and difficult to represent in a graphical reconstruction. Its relations to the visceral arches, however, can be shown quite accurately. It communicates with the pharynx by a slit-like opening elongated in a cranio-caudal direction, the posterior part of which is common to both 1st and 2nd visceral pouches. Dorsally it is extended into a more or less pointed extremity (fig. 2, $P_1.D.$) which is still connected to the ectoderm by a strand of cells. This strand of cells indicates the final point of closure of the cleft and is situated cranial and slightly dorsal to the columella. Laterally the pouch is pinched between the quadrate in front and the ceratohyal behind, so that from the side it presents a crest lying between these two structures. The position of this crest is indicated by a line ($P_1.R.$) in the reconstruction (fig. 2). Medially the first pouch is overlapped a little by the second, so that, as was stated above, they have to some extent a common opening into the

pharynx. This overlapping makes it appear in a graphical reconstruction as though a dorsal pocket of the second pouch belonged to the first; that this is not so is clearly shown by the courses of the VIIth and of the IXth nerves, for the pocket in question lies between the two nerves. It must, nevertheless, be admitted that these pouches are very unsatisfactorily shown in a plane graphical reconstruction from this aspect.

The course of the VIIth nerve and its relation to the columella must now be described. It emerges from the skull through a notch in the cranial and ventral part of the otic capsule, and at once swells to form the geniculate ganglion. From this the ramus palatinus passes cranially, and the ramus hyomandibularis, which is alone of importance for the purposes of this paper, caudally. The latter crosses dorsal to the columella, lying medial to the processus dorsalis (figs. 1 and 2, *VII HM.*), and then curves ventrally to run close behind the ceratohyal. It ends by breaking up into branches which supply the hyoid musculature.

The chorda tympani nerve arises from the ramus hyomandibularis before it has crossed the columella. It runs caudally to cross the columella lateral to the ramus hyomandibularis but medial to the processus dorsalis. It then diverges in a lateral direction and curves round the dorsal end of the processus dorsalis, finally running cranially and dorsal to the lateral division of the columella. It reaches the caudal border of the quadrate which it follows in a ventral direction. Beyond this it was impossible to trace the chorda tympani with any certainty in this particular embryo. From older embryos it is clear that it had the usual course, i.e. twisting round to the inner aspect of the quadrate and then, after passing the mandibulo-quadrate joint, running forwards medial to Meckel's cartilage. The first part of its course is shown in the reconstruction (fig. 2).

There was another branch from the ramus hyomandibularis which was at first taken to be the chorda tympani. It originated from the main trunk just after crossing the columella, and ran laterally in close association with the true chorda tympani. It could not be traced further forwards, however, than the level of the processus dorsalis, and is probably the representative of some twigs which were found in a similar position in the alligator embryos. These twigs supplied the muscles of the ear-flap.

The relationship of the columella to the chief blood-vessels of this region must be mentioned in passing. The most conspicuous vessel is the vena capitis lateralis. It runs in a cranio-caudal direction dorsal to the medial division of the columella and internal to the processus dorsalis. The internal carotid artery runs cranially, ventral and medial to the foot-plate of the columella. It gives a temporo-orbital (Hochstetter, Shiino) branch which runs in a dorsal and slightly cranial direction posterior to the columella. This vessel probably corresponds with the facial artery which Versluys (1898) describes in many Lacertilia.

Crocodile I

This embryo presented almost exactly the same external appearance as the one just described. The chondrocranium and skeleton generally differed a little in that chondrification was rather less advanced, although no absolute distinction could be made out. The otocyst was clearly in a less developed state however, since the semicircular canals had not been completely separated off. Their future position was clearly indicated.

The columella (fig. 3), which is still largely blastemal, showed just the same parts as were seen in Crocodile II. It differed in that the foot-plate was all

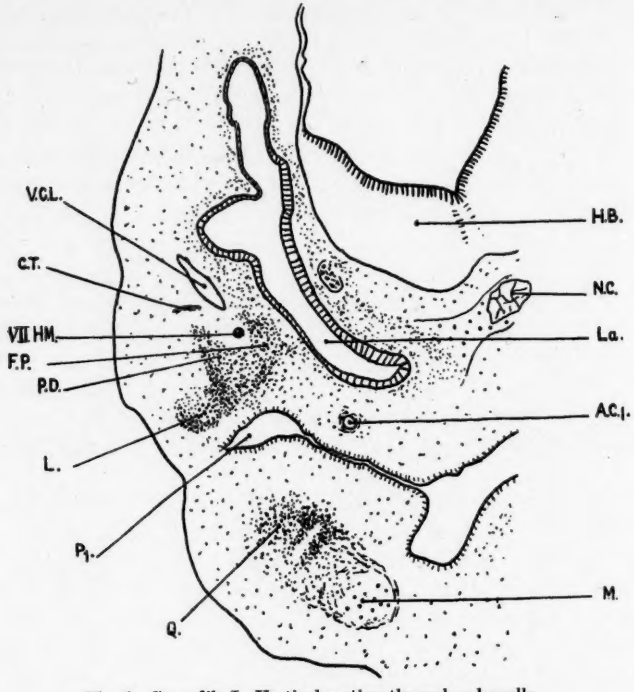

Fig. 3. Crocodile I. Vertical section through columella.
(For lettering see p. 304.)

but indistinguishably fused with the otic capsule; without the centre of chondrification which had already appeared it is doubtful whether any boundary between the two structures could have been found. The centre for the processus dorsalis was present, but by no means obvious. It seems that it appears rather later than the other two centres in the columella.

The ceratohyal was entirely pro-cartilaginous, and kinked in the same curious manner. Its dorsal connection was less clearly shown on account of the inconvenient plane of section in this region. It appeared to be attached

to both parts of the columella at their points of junction, although from the evidence of Crocodile II it is probable that the real connection was with the lateral division only. Ventrally the fairly well-defined part of the ceratohyal ended abruptly some little distance dorsal and caudal to the retroarticular process of Meckel's cartilage; it was continued by a little very slightly condensed blastema which could be traced with difficulty into the process mentioned above. The appearance was quite different from the direct continuity between Meckel's cartilage and the ceratohyal which is so characteristic of later stages.

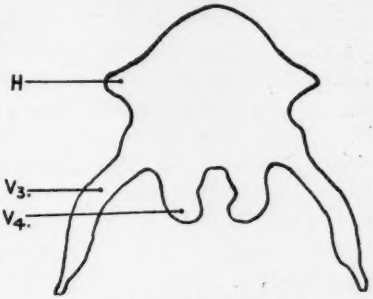

Fig. 4. Crocodile I. Graphic reconstruction of the body of the hyoid and visceral arches from the ventral aspect.
(For lettering see p. 304.)

The basi-lingual cartilage does not differ in any important particular from the same structure in Crocodile II, and the description already given will serve equally well for both. A graphical reconstruction is given in fig. 4.

The pharyngeal pouches also do not require special mention. In degree of development and in relationships they are almost identical with those of Crocodile II. For the same reason it is unnecessary to describe the nerves and blood-vessels round the columella. It may be observed, however, that the second branch from the ramus hyomandibularis in this embryo leaves the parent trunk well caudal to the columella, and that there is no question of confusing it with the chorda tympani. The latter has the typical course and relations.

Crocodile III

This embryo is distinctly more advanced than the former two. The 2nd and 3rd visceral arches are no longer clearly visible externally. The 1st pharyngeal pouch has lost its connection with the ectoderm, while the 2nd, although still connected to the ectoderm, is no longer open. Chondrification is well forward in most parts of the skull, but is still incomplete in the otic capsule and visceral skeleton.

The columella consists of embryonic cartilage which is not yet typically hyaline. It no longer shows a segmentation into medial and lateral divisions, although if a trace of the original boundary were present, it would probably be missed since the sections are transverse to the long axis of the columella. The foot-plate is fused with the wall of the otic capsule, although doubtful traces of a separate origin can be found. The lateral end of the columella has undergone considerable modification. Besides the processus dorsalis two further processes have been developed, an infra- and an extra-stapedial. The extrastapedial appears simply as a lateral prolongation of the stem of the columella towards the ectoderm. The infrastapedial (fig. 5, *I.St.*) originates

from the columella in approximately the same sagittal plane as the processus dorsalis, perhaps a little further laterally. It is a thin incompletely chondrified process which passes caudally and slightly ventrally to join the top of the ceratohyal. In a few sections a distinct boundary can be seen between its proximal end and the base of the processus dorsalis (i.e. the lateral extremity of the medial division of the columella), and this is probably the last indication of its origin from the lateral and not from the medial division of the columella. The processus dorsalis is a stout projection from the columella near its lateral end, which still shows signs of its separate centre of chondrification. It reaches nearly to the otic process of the quadrate, but is unconnected with it.

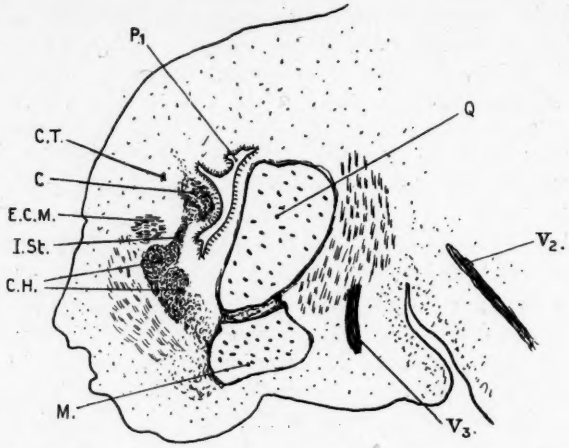

Fig. 5. Crocodile III Sagittal section through the columella and ceratohyal.
(For lettering see p. 304.)

The ceratohyal (fig. 5, *C.H.*) is an irregular strand of incompletely chondrified blastema which passes ventrally from the extremity of the infrastapedial to the retroarticular process of Meckel's cartilage. The kinking which was observed in Crocodiles I and II is still strongly marked. Fusion with Meckel's cartilage is almost complete, but several layers of slightly flattened cells with sharply marked outlines still mark the boundary between the two structures.

The basi-lingual cartilage has not altered very much; it is less completely chondrified than are most parts of the skull, but shows a distinct advance over Crocodiles I and II. It lies in the same position beneath the larynx. The hyoid processes are well shown and are approximately ·5 mm. in length, and the 3rd visceral arches are strongly developed structures. The two processes which were mentioned above as originating from its hinder border and lying on either side of the trachea are very poorly developed; it is in fact doubtful whether they are present at all in this embryo.

It is unnecessary to describe the pharyngeal pouches, nerves, etc., in this

embryo, since they do not differ essentially from the corresponding structures in Crocodiles I and II. It may be pointed out that the form of the pouches has altered considerably, e.g. the dorsal pocket of the second pouch can no longer be found, but this has no bearing upon the development of the columella. There is one new development to which a few words must be given, viz. the hyoidean musculature. The main part of this consists of a large belly which passes from the parotic region of the skull towards the retroarticular process of Meckel's cartilage. Near its upper end there is a small part, incompletely separated from the main mass, which will differentiate into the extracolumellar muscle (fig. 5, ***E.C.M.***), and the muscles which move the ear-flap. The fibres of this part are distinguishable because they pass in a lateral cranial and ventral direction towards the infrastapedial and the dorsal end of the ceratohyal, instead of in a ventral and caudal direction as do the fibres of the main muscle mass. The fibres of the extracolumellar muscle lie entirely external to the ramus hyomandibularis of ***VII***.

Alligator II

This embryo will be described before Alligator I for the same reason that Crocodile II was described before Crocodile I. Actually there is so little difference between the two stages that one description would serve almost equally well for either.

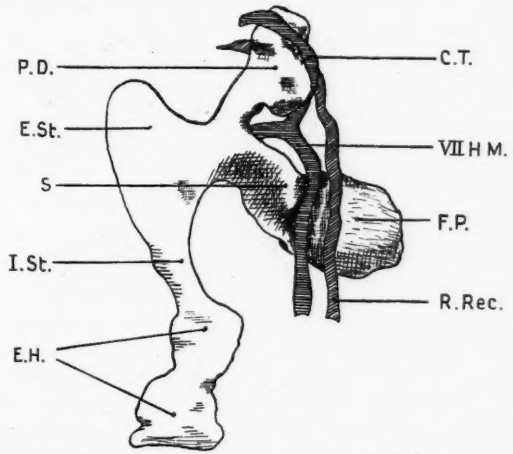

Fig. 6. Alligator II. Drawing from wax-plate reconstruction of columella, ramus hyomandibularis of ***VII***, chorda tympani, and ramus recurrens ad trigeminum. Postero-lateral aspect of left side.

(For lettering see p. 304.)

Alligator II is considerably further advanced than Crocodile III. The whole of the chondrocranium and visceral skeleton has been converted into typical hyaline cartilage, and ossification has begun in the squamosal and pterygoid

bones; the pharyngeal clefts are all closed and the pouches no longer have any connection with the ectoderm; externally no indication of the 2nd and 3rd visceral arches can be seen, and a well-marked depression, overhung from above and behind by a flap, has been formed in the region of the future tympanum.

A wax-plate reconstruction was made of the columella and neighbouring structures in this embryo (fig. 6). Unfortunately, no guiding plane had been embedded, so that there is probably a little distortion of structures from their natural position owing to inaccuracy in piling the plates. This distortion does not appear to be serious.

The columella is now a continuous cartilaginous element possessing already all the main features of the adult as far as shape is concerned. It consists of

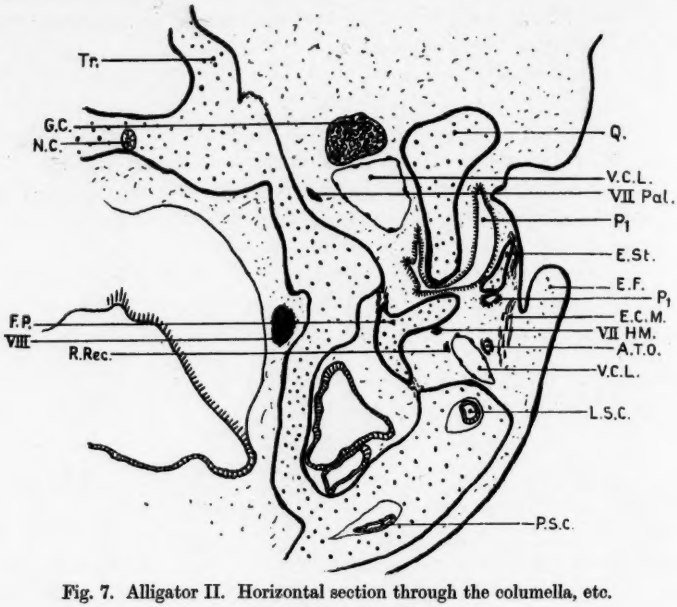

Fig. 7. Alligator II. Horizontal section through the columella, etc.
(For lettering see p. 304.)

a foot-plate, a stem, and three lateral processes, processus dorsalis, extrastapedial and infrastapedial.

The foot-plate (fig. 7, *F.P.*) is an oval cartilage fitting into the fenestra ovalis. Ventrally it is in close connection with the margin of the fenestra, although even here there is no continuity between foot-plate and capsule. For the rest of its circumference the foot-plate is fairly widely separated from the margin of the fenestra, although attached to it by connective tissue.

The stem originates from near the cranial end of the foot-plate. It is a

cylindrical cartilage which tapers a little as it passes in a lateral and slightly dorsal direction (fig. 6, *S.*).

The processus dorsalis (fig. 6, *P.D.*) is a more or less triangular cartilage attached by its apex to the extremity of the stem and running in a dorsal and slightly caudal direction. It ends dorsally very close to the otic process of the quadrate with which it is as yet unconnected. Its caudal border is notched close to its dorsal extremity by the chorda tympani nerve which hooks round it here. There are indications that the processus dorsalis is becoming segmented off from the stem of the columella, but these are not very clear.

The extrastapedial (figs. 6 and 7, *E.St.*) and infrastapedial (fig. 6, *I.St.*) together form a large fan-shaped cartilage projecting cranially and laterally. The handle of the fan is in direct continuity with the stem of the columella, while the long slightly curved lateral border (which is directed dorso-ventrally), is applied in its upper two-thirds to the ectoderm of the future tympanic membrane. This part which is applied to the ectoderm is the extrastapedial. The infrastapedial originates from the ventral end of the lateral curved border and partly from the ventral border itself, and runs almost directly ventrally as a slender cartilaginous rod. It ends in a nodule of incompletely chondrified blastema which will be described in connection with the ceratohyal.

The ceratohyal is a simple rod of cartilage directly continuous with the retroarticular process of Meckel's cartilage. It lies behind the quadrate and is separated from it by the lateral crest of the 1st pharyngeal pouch. This crest has almost the same extent and relations as is shown in the reconstruction of Crocodile II (fig. 2, $P_1.R.$). The ramus hyomandibularis of VII lies immediately behind the ceratohyal. Superiorly the ceratohyal can be followed into two incompletely chondrified nodules of blastema; they are shown in the wax-plate reconstruction (fig. 6, *E.H.*), but better in a graphical reconstruction of this region alone (fig. 8). These nodules undoubtedly represent what Parker has called the "epihyal," but whether they can justly be described as a distinct morphological element must be discussed later.

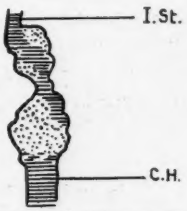

Fig. 8. Alligator II. Graphic reconstruction of the junction between the ceratohyal and infrastapedial. Lateral aspect of left side.

Horizontal lines—cartilage. Stippled areas — condensed blastema.

(For lettering see p. 304.)

The basi-lingual cartilage consists of a median trough-shaped plate with its cranial border lying ventral to the larynx, and with three processes from each lateral border. The most anterior of these is short and rather indefinite in outline. It represents the ventral end of the hyoid and has no connection with any other part of the skeleton. The second process, the 3rd visceral arch, is large and well chondrified; it extends round the sides of the pharynx and slightly forwards over its dorsal wall. The third process is an ill-defined continuation of the postero-lateral angles of the median cartilage for a short distance dorsally, caudally, and laterally. It probably represents the 4th visceral arch.

Very little need be said about the other structures in this embryo. The 1st pharyngeal pouch is large, and, except for a small diverticulum ventral and caudal to the columella (fig. 7, P_1.), is entirely anterior to the columella and the structures connected with it. Nerve relationships remain essentially the same as in the crocodiles. One new nerve, however, has made its appearance. This is a stout caudal branch from the gasserian ganglion which takes a similar course to the ramus hyomandibularis of VII. At first it lies lateral to this nerve, but crosses it dorsally to its medial side as it passes the columella, and finally joins the superior cervical ganglion of the sympathetic. It communicates with the ramus hyomandibularis of VII and with the jugular ganglion. Shiino (1914) mentions this nerve and recognises it as sympathetic, but does not name it. Bender (1906) calls it the "ramus recurrens ad trigeminum." The course of the chorda tympani is typical, and does not need a special description. It may be well to point out that it is not quite the same as is shown in Shiino's Fig. 33, p. 352, for *Crocodilus biporcatus*. In this species, apparently, the chorda tympani loops dorsally well above the processus dorsalis of the columella. In my embryos it loops round the dorsal end of the processus dorsalis in a slight groove (fig. 6, *C.T.*). Its subsequent course is the same in both cases, i.e. first lateral, then caudal and finally medial to the caudal border of the quadrate.

The extracolumellar muscle has been completely separated from the rest of the hyoid musculature. It arises from the crista parotica, whence its fibres diverge in a cranial direction to an extended insertion into (1) the posterior margin of the tympanum (fig. 7, *E.C.M.*), (2) the ventral end of the infrastapedial process, and (3) the incompletely chondrified blastema of the epihyal.

Alligator I

This embryo is almost identical with Alligator II, and it is unnecessary to describe it. The epihyal is rather more clearly shown (fig. 9, *E.H.*), for here it consists of a nodule of incompletely chondrified blastema connected on both sides by short tracts of blastema quite free from cartilage with the infrastapedial and ceratohyal respectively. No clear discontinuity between the processus dorsalis and the rest of the stapes is shown.

Alligator III

In this embryo ossification is well advanced in the membrane bones of the skull generally, although none of the cartilage as yet shows signs of replacement by bone. It is slightly older than the 13 mm. skull of *Crocodilus biporcatus* reconstructed by Shiino. The illustrations which he gives would apply quite well to this embryo.

The columella and its associated structures do not show any important changes. It is still entirely cartilaginous, and no trace of the later division into a medial columella and a lateral extracolumella is visible. The processus dorsalis is in direct cartilaginous continuity with the stem. The infrastapedial

is a slender process flattened cranio-caudally. Its ventral end is kinked backwards where it receives part of the insertion of the extracolumellar muscle. From this point it runs in a ventral direction as a round cartilaginous strand, which swells after a short distance to form a distinct nodule, the epihyal. Cartilage is continuous from the infrastapedial through the epihyal with the ceratohyal, which is itself indistinguishably fused with the retroarticular part of Meckel's cartilage.

In the basi-lingual cartilage no change has occurred, except that the processes which represent the ventral extremities of the two hyoid arches are relatively much smaller and more difficult to identify.

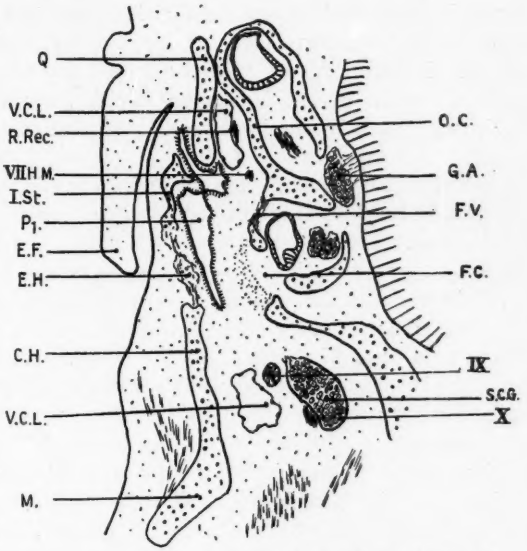

Fig. 9. Alligator I. Vertical section caudal to the columella.
(For lettering see p. 304.)

The columella is now almost completely surrounded by the tympanic part of the 1st pharyngeal pouch. There is a large pocket lying cranial and dorsal to the columella which nearly meets a smaller pocket which has developed in a caudal and ventral position. A long pocket has been formed which passes ventrally between the ceratohyal and the quadrate, to end blindly in a little depression in Meckel's cartilage median and caudal to its surface for articulation with the quadrate. This is the "siphonium" or "pneumatic duct" of the adult.

Alligator IV

This embryo is far more advanced than any of those described hitherto. The adult form of the head has been attained in all its essential features, and

ossification is nearing completion in the cartilage as well as in the membrane bones.

The shape of the columella roughly corresponds with that of the columella in Alligator II. Ossification has begun in the foot-plate, and extends laterally about half-way along the stem. The cartilaginous lateral half of the stem is no longer directly continuous with the processus dorsalis, extrastapedial, and infrastapedial. These three processes together constitute the part of the auditory apparatus which is called the "extracolumella" in the adult and they will be referred to in future by that name. The medial stem and foot-plate will be referred to as the "stapedial part" of the columella. In this embryo the division between the extracolumella and the stapedial part is marked by a layer of densely packed cells which stain deeply with haematoxylin. It must be noted that, as Versluys (1903) pointed out for Lacertilia, this point does not correspond with the boundary between the medial and lateral divisions of the columella in early stages. This primary division lay lateral to the processus dorsalis, whereas this new boundary lies medial to the processus dorsalis.

The Extracolumella. The processus dorsalis is roughly triangular in shape and has its long axis directed dorsally and caudally. Its curved dorso-caudal border is swollen slightly and lies in the margin of the tympanum. It is closely connected by ligaments with the otic process of the quadrate. Its apex is almost continuous with the base of the extrastapedial process and the lateral end of the stapedial part of the columella. There is a definite boundary separating it from the last-named structure, however, as was described above. There are, moreover, signs that it is becoming detached from the base of the extrastapedial in that its connection with this element is slight and partly fibrous; macroscopic examination of the older Alligator V gave no confirmation of this observation. The extrastapedial and infrastapedial together form a fan-shaped cartilage very like that described for Alligator II (fig. 6). Its long slightly curved lateral border lies entirely in the tympanum and is horizontal instead of vertical, as it was in the younger embryo (compare figs. 6 and 10). There are in addition cranial and caudal borders. The cranial border is considerably thickened, forming what appears to be a continuation of the stem; this is the extrastapedial part. The infrastapedial is a slender laterally compressed strand of cartilage which runs caudally in the tympanum from the caudal border of the main cartilage.

The epihyal is an irregular nodule of cartilage lying on the quadrate close to the caudal margin of the tympanum. It is apparently pierced by a foramen latero-medially. Cranially it is in very close contact with the infrastapedial, but not in direct continuity with it. The two structures are bound together by connective tissue. Dorsally it is connected by a dense mass of connective tissue fibres with the margin of the tympanum and also with the caudal angle of the processus dorsalis. Ventrally it passes without a break into the ceratohyal, a cylindrical mass of hyaline cartilage lying in a groove between the

quadrate and the exoccipital. The ceratohyal cannot at this stage be traced into the mandible; as it is followed ventrally it becomes fibrous and blends with the sheath of the siphonium or pneumatic duct. The latter is a tube which extends from an air cell in the quadrate to connect with a further air cell in the mandible.

Alligator V

From a dissection of Alligator V little of any importance was discovered. The external form of the extracolumella, however, was well shown (fig. 10). The connection between the epihyal and the processus dorsalis did not appear to be any more than the thickened connective tissue margin of the tympanum, while its connection with the infrastapedial must have been very slight since the least violence was sufficient to detach the one from the other. The swollen

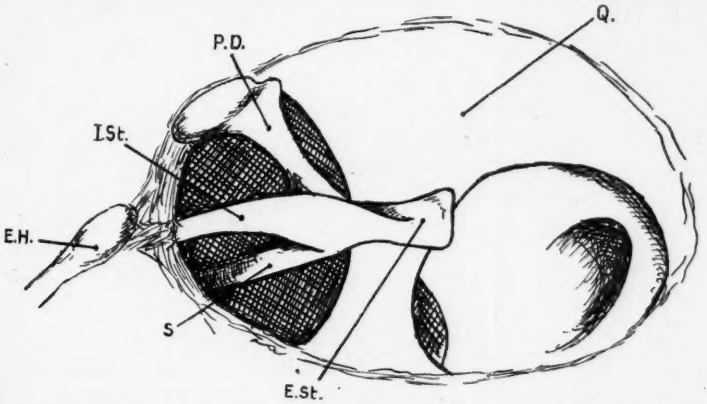

Fig. 10. Alligator V. Lateral view of tympanic cavity after removal of tympanum and of most of the squamosal bone. Right side. From a dissection.

(For lettering see p. 304.)

dorso-caudal border of the processus dorsalis had rather the appearance of a separate cartilage; it was very easy to detach it from the rest of the process, but nevertheless cartilaginous continuity was probably complete: it certainly was in Alligator IV.

3. CONNECTED ACCOUNT OF DEVELOPMENT OF COLUMELLA

The development of most skeletal elements can be divided into three well-marked stages: blastemal, cartilaginous and bony. The terminations of the first and second stages are indicated by the appearance of centres of chondrification and of ossification respectively, while the third stage lasts until the final adult structure has been attained. The embryos described above belong mainly to cartilaginous and bony stages, although Crocodiles I and II are still blastemal so far as many structures are concerned. Earlier blastemal stages have been investigated only by Shiino (1914), who described an embryo of

Crocodilus biporcatus with a head length of 5 mm. For the sake of completeness a summary of his facts must be given.

He found that the blastemal primordia of the hyoid and mandibular arches, and also of the otic capsule, were already plainly visible. The caudal and dorsal end of the hyoid blastema was bent medially behind the 1st pharyngeal pouch towards the otic capsule to form the columella. Its medial end was closely applied to the otic capsule, but could be distinguished from it sufficiently clearly to show that the columella was entirely hyoidean in origin. There was apparently no differentiation either within the columella, or between it and the hyoid blastema. Anteriorly and ventrally the hyoid blastema was indistinguishably fused with the overlying mandibular blastema. My own embryos follow closely on this stage.

The cartilaginous stage begins with the appearance of two centres of chondrification, one medial and close to the otic capsule, and one in the extreme lateral end of the columella. At the same time a distinct boundary is formed separating the columella into medial and lateral divisions. This boundary lies much nearer the lateral centre of chondrification than the medial. The centre for the processus dorsalis probably appears later than the other two, for Shiino describes an embryo of from 6–7 mm. head length in which it is not indicated, although both medial and lateral centres have appeared. In my youngest embryos all three centres are present together, although that in the processus dorsalis is less advanced than the others. The processus dorsalis is quite clearly connected with the medial division of the columella, as was described by Versluys (1903) in many Lacertilia, and by Kingsley (1900) for the alligator, but is as yet unconnected with the quadrate or with the otic capsule. The medial division of the columella is very closely applied to the otic capsule, and is distinguishable only because of its centre of chondrification. The only connection of the lateral division is with the blastema of the rest of the hyoid arch (the future epihyal and ceratohyal).

As chondrification proceeds the division between the medial and lateral divisions of the columella vanishes, and at the same time an extrastapedial process, which points laterally and slightly cranially, is developed. Its extremity lies beneath the area of ectoderm which will form the outer layer of the tympanum. The blastema of the epihyal and ceratohyal has differentiated into a short thin proximal part attached to the base of the extrastapedial process, and a thicker distal part which abuts on the retroarticular process of Meckel's cartilage. This distal part shows a very characteristic kinking at this stage. The epihyal and ceratohyal both chondrify rather later than the columella. It is difficult to say at this stage (i.e. the beginning of the cartilaginous stage) whether or not the ceratohyal is really fused with Meckel's cartilage. The appearance of Crocodile I is distinctly against this interpretation, although a little slightly condensed blastema does perhaps connect the two structures. The same condition is shown, but is less striking, in Crocodile II. It is possible that the difficulty in following the ceratohyal into the mandible may be due

in part to the very pronounced kinking in the ceratohyal at this point. This kinking is clearly shown in the reconstruction (fig. 2). Again, it may be that the apparent discontinuity in Crocodile I is simply the result of incipient chondrification, just as the differentiation of medial and lateral divisions in the columella is. Shiino's description of an early blastemal stage favours this last interpretation since he found then complete continuity between the ceratohyal and the mandible. I cannot think that this is the right interpretation, however, because the boundary between the ceratohyal and Meckel's cartilage is quite different in appearance from the boundary between the medial and lateral divisions of the columella, and, moreover, no distinct centres of chondrification have appeared in this region of the ceratohyal. At least one is justified in stating that the ontogenetic evidence of Crocodile I, and in a less degree that of Crocodiles II and III, strongly indicates that the apparent continuity of Meckel's cartilage and the ceratohyal is not a primary phenomenon, but has been brought about by fusion. To settle this point a reinvestigation of blastemal stages is highly desirable.

With advancing chondrification all boundaries within the columella disappear, and also the boundary between the ceratohyal and Meckel's cartilage. The region connecting the infrastapedial and the ceratohyal remains blastemal longer than any other, and when it is finally chondrified forms Parker's epihyal. Whether this element really has at any time a separate existence is doubtful, although its cartilage was not directly continuous either with that of the infrastapedial or of the ceratohyal in Alligator I. In all the other embryos it was continuous with one or the other, and in the later stages it forms simply the swollen dorsal end of the ceratohyal. This was the condition observed by Peters (1870) and Huxley (1869). Probably it is simply a region of the hyoid blastema in which chondrification is delayed for some reason; perhaps because of the insertion of the lowermost fibres of the extracolumellar muscle. There can be no harm in retaining the term epihyal, however, provided no homology is implied in its use. A swelling in this position is certainly characteristic of crocodiles, although it is not shown as such a clearly distinct element in any of the foregoing embryos as in Parker's figures.

Towards the end of the cartilaginous stage and at the beginning of the bony stage signs of a resegmentation of the columella are evident. The most important is the beginning of a segmentation of the columella into extracolumellar and stapedial parts. The division forms at the lateral end of the stem just medial to the origin of the processus dorsalis. At the same time the epihyal becomes separated from the infrastapedial (although its former continuity is still indicated by the presence of connective tissue) and acquires a ligamentous connection with the processus dorsalis. Parker describes this transformation in his 7th stage, where he also finds that the distal extremity of the processus dorsalis has been separated from its stem. There was some indication of this in Alligator II, but too doubtful to afford any confirmation for Parker's statement. At the same time there has been a rotation of the extra- and infra-

stapedial processes so that they lie now in a horizontal instead of in a vertical plane. Ossification has started in the foot-plate and stem of the stapedial part of the columella, but there is no indication of separate centres of ossification for these two parts (i.e. foot-plate and stem) as was described by Parker.

4. DISCUSSION

The crocodilian columella with its stapedial and extracolumellar divisions is unquestionably homologous with the columella of the Lacertilia. Versluys, among many others, has shown that the lacertilian columella develops from the dorsal end of the hyoid arch, and that probably the otic capsule takes no part in its formation; further, that it chondrifies from three centres, one for the foot-plate, one for the extracolumella and one for the processus dorsalis, and all three are at one stage in direct cartilaginous continuity. Again, when the division between extracolumella and stapes appears, it is formed medial to the origin of the processus dorsalis and does not correspond to the primary division separating the two centres of chondrification. This primary division was lateral to the processus dorsalis. With regard to the otic or hyoidean origin of the medial end of the columella there has been considerable difference of opinion. Although in some cases, e.g. Platydactylus and Gecko (Versluys, 1903), there is a clear boundary between the medial end of the columella and the otic capsule, yet in other forms, e.g. Lacerta (Versluys, 1903; Cords, 1909), no such boundary can be found. Versluys comes to the conclusion that a separate hyoidean origin for the columella is primitive, while Fuchs (1909) maintains the opposite, namely, that the medial end of the columella arose primitively from the otic capsule. In view of the fact that boundaries between skeletal elements which were undoubtedly distinct phylogenetically are frequently invisible in blastemal stages (e.g. between the human clavicle and the sternum), no decision of this question can be hoped for from purely embryological investigations. In the embryos described above the boundary, such as it is, is quite probably simply the result of the appearance of a centre of chondrification, although Shiino claims to have found a boundary before any centre has been formed.

Clearly this point with regard to the otic or hyoidean origin of the medial end of the columella is too indeterminate to be of use in a comparison, but in all the other characteristics mentioned above the lacertilian columella is in complete agreement with the crocodilian. At the same time it may be said that the relationships to nerves, blood-vessels, and the tympanic cavity are essentially the same in both groups, and do not need recapitulation.

The crocodilian columella differs from the lacertilian on two main points: (1) the fate of the processus dorsalis, (2) the possession of an epihyal and ceratohyal. Bound up with this second difference is the question of the homology of the processus internus (Versluys' term) of the Lacertilia, which is lacking in the Crocodilia unless the epihyal and ceratohyal together are its homologues.

1. ***Processus dorsalis.*** Versluys states that in the Lacertilia generally the processus dorsalis comes into close contact with the parotic region of the skull, with which it finally fuses and becomes detached from the columella. In a few cases a ligament remains to indicate its origin. The detached processus dorsalis he calls the "intercalary cartilage." Gaupp calls Versluys' parotic process "crista parotica," and the intercalary "processus paroticus." Rice (1920) describes the intercalary (i.e. the processus paroticus of Gaupp) as being at no time in connection with the columella in the skink. The processus dorsalis of crocodiles, on the other hand, is connected only with the otic process of the quadrate (it may occasionally be fused with it; e.g. Shiino) and does not actually become separated from the columella. The beginnings of such a separation are sometimes visible, as was shown by Alligator IV. Peters (1868) described in a specimen of *Crocodilus acutus* a processus dorsalis (called by him malleus) which was separate from the columella but connected with it by a small separate cartilage which he homologised with the lenticular. Parker (1883) found in embryos of *Crocodilus palustris* (5th and 7th stages) that the processus dorsalis (his suprastapedial) was in two parts, a stem attached to the extracolumella and a nodule of cartilage lying in the border of the tympanum and attached by a ligament to the epihyal. It would seem that division may occur in two places in the processus dorsalis; near the dorsal extremity, and again close to the extracolumella. The "stem" of the processus dorsalis lying between these two divisions probably represents Peters' lenticular, and possibly also the ligament which is found in some Lacertilia connecting the intercalary with the extracolumella. This division of the processus dorsalis, although by no means an invariable characteristic of the Crocodilia, is undoubtedly the same process which has been brought to completion in most Lacertilia. The difference, therefore, is one of degree only. The connection of the processus dorsalis of crocodiles with the otic process of the quadrate instead of with the crista parotica is not, however, a difference of degree. Nevertheless, little importance can be attached to it, for assuming, as is highly probable, that the processus dorsalis is a structure acquired for the first time in the class Reptilia, there seems no reason why it should not become connected with the quadrate in one sub-class and with the crista parotica in another. The otic process of the quadrate articulates with the crista parotica, so that these two parts are in very close relation to each other.

2. ***Ceratohyal and Epihyal.*** Concerning the homology of these parts there has been considerable difference of opinion. Peters (1868) and Gadow (1888, 1901) have found in them the representative of the processus internus of Lacertilia. Huxley (1869), Parker (1883), Versluys (1903), and Shiino (1914), and indeed most anatomists, have regarded them as the homologue of the hyoid of Lacertilia, and if this is true, it follows that the processus internus must be lacking in crocodiles. It may be remarked here that the processus internus of Kingsley (1900) is undoubtedly the processus dorsalis. This was pointed out by Van der Klaauw (1924). Kingsley homologised the ceratohyal

and epihyal with the neck of the malleus in mammals, saying that it arose *in situ* and was unrelated either to the hyoid or to the processus internus. Whatever evidence there may have been in favour of this view has now either received a different interpretation or has been discredited altogether, so that it is unnecessary to discuss it here.

At first sight it certainly appears that the ceratohyal and epihyal correspond to the upper part of the lacertilian hyoid, which is continuous with the extracolumella in early embryonic stages. On the other hand, it has been urged, notably by Gadow (1888), that the complete fusion between the ceratohyal and Meckel's cartilage in crocodiles, and its complete separation from the hyoid cornua of the basi-lingual cartilage even in earliest stages, are most unlikely if the former is really the representative of the lacertilian hyoid. As an alternative it was suggested that the epihyal and ceratohyal are the homologues of the processus internus of Lacertilia, otherwise unrepresented in crocodiles. Now Versluys has shown that the processus internus of Lacertilia develops as an outgrowth from the primary medial division of the columella, that it appears late in ontogeny compared with such structures as the lacertilian hyoid or the crocodilian ceratohyal, and that it has no separate centre of chondrification. Embryonically it is unconnected with Meckel's cartilage (Versluys), although both Gadow and Peters stated that a thin ligamentous connection running ventrally between the quadrate and pterygoid bones may be present in the adult. Versluys stated further that it lay entirely anterior to the 1st pharyngeal pouch. In view of the work of Goodrich (1915), who showed that it was possible for a structure (e.g. the chorda tympani) to be post-trematic and yet pre-tympanic, this statement may be found to require modification. It can be said with certainty, however, that the processus internus is pre-tympanic.

In every one of these particulars the processus internus is in direct contrast with the ceratohyal and epihyal of crocodiles, and in face of this contrast it seems impossible to maintain the homology.

In comparing the ceratohyal and epihyal with the lacertilian hyoid there are one or two minor differences which must be considered before discussing the more important differences mentioned above. The hyoid of Lacertilia is connected to the columella in early stages by a strand of blastema, the interhyal, which does not chondrify, so that later in development the hyoid becomes quite free from the columella. In crocodiles the dorsal end of the ceratohyal is swollen to form what Parker identifies as a separate element and terms "epihyal," and is in direct continuity with the columella through the infrastapedial process. This infrastapedial process is clearly simply a chondrified interhyal, while the development of an epihyal is a specialisation which can have no important bearing on the main question. There is a further resemblance between the upper end of the ceratohyal, or epihyal, and the lacertilian hyoid, in that the former tends to become separate from the infrastapedial (= interhyal) and to gain an attachment to the processus dorsalis. In many lacertilia

the hyoid, having become free from the columella, acquires a connection with the intercalary (= processus dorsalis) on the crista parotica of the skull.

With regard to the continuity between Meckel's cartilage and the ceratohyal, the crocodiles described above indicate strongly that it is secondary. The association between the two structures, particularly in Crocodile I, is not nearly so close as that between the medial end of the columella and the otic capsule; on the other hand, Shiino describes a complete continuity in an earlier blastemal stage. One cannot help feeling that perhaps the attempt to obtain a decisive answer on embryological grounds is as futile as it was over the question whether the medial end of the columella was hyoidean or otic in origin. However, with the exception of Shiino's isolated observation, the evidence certainly inclines one to the view that the connection is secondary, and it seems fair to adopt this position provisionally. In the light of Versluys' observation that in Lacerta the developing hyoid lies very close to Meckel's cartilage, and that in Geckos there is a ligamentous connection between the two arches, it does not seem improbable that in another sub-class of the same class of animals the two structures might fuse. Consequently when, in such a sub-class, a structure is found which agrees in almost all other respects with the hyoid of Lacertilia, but is found to be connected, probably secondarily, with Meckel's cartilage, the conclusion is inevitable that homologous structures are being dealt with. The "other respects" in which the ceratohyal agrees with the lacertilian hyoid may be recapitulated as follows: It develops in the blastema of the hyoid arch, and is connected with the lateral division of the columella. It tends to lose this connection and to become connected to the processus dorsalis (= intercalary). It has, moreover, all the relations which would be expected of it as the homologue of the hyoid, particularly as regards the 1st pharyngeal pouch. There remains only one absolute distinction between the two structures, namely, that the ceratohyal is from the earliest stage investigated (Shiino, *Crocodilus biporcatus* of 5 mm. head length) quite unconnected with the short hyoid cornua of the basi-lingual cartilage. Possibly still younger embryos may show that this discontinuity is not so absolute as it appears to be, but however that may be, as a single difference it is not sufficient to overthrow a homology based upon the numerous resemblances mentioned above.

This argument cannot claim to be new. In its essentials it was given in 1903 by Versluys, but it has seemed worth while to give a recapitulation of it, amplified and supported by the facts which have been discovered since then. If it is correct it disposes of the arguments drawn by Peters and Gadow from the condition in the crocodile in support of the homologies which they assigned to the mammalian ossicular chain. Peters assumed that the crocodilian ceratohyal was a continuation of Meckel's cartilage homologous with the region of Meckel's cartilage in mammals which joins the malleus during embryonic life. Gadow looked upon it as the representative of a ligamentous or articular connection which exists in certain Elasmobranchs between the hyomandible

and the lower jaw, and, with Peters, considered it to be homologous also with the region of Meckel's cartilage in mammals mentioned above. It seems, however, that these views are now untenable, and that, provided the crocodilian ceratohyal, the lacertilian hyoid and the mammalian hyoid are all homologous structures, the crocodilian condition has no special bearing on the question of the homologues of the malleus, incus and stapes in the Sauropsida.

5. SUMMARY

The columella of the Crocodilia develops from the dorsal part of the hyoid blastema. It is probably impossible to say definitely on embryological grounds whether the otic capsule takes any part in the formation of its medial end or not.

It chondrifies from three centres, one in the foot-plate, one in its lateral extremity, and one in the processus dorsalis. This last centre appears later than the other two. At this stage the columella shows a segmentation into medial and lateral divisions; the processus dorsalis is connected to the medial division.

Except for the complete absence of a processus internus, the development of the crocodilian columella is essentially similar to that of the lacertilian.

The ceratohyal and epihyal develop in the hyoid blastema; it is doubtful whether the epihyal is really an independent element since it almost always appears as the swollen dorsal end of the ceratohyal. In blastemal or early cartilaginous stages the fusion between the ceratohyal and Meckel's cartilage is incomplete.

The ceratohyal is almost certainly homologous with the lacertilian hyoid, but differs from it in that it is unconnected with the short hyoid cornua of the basi-lingual cartilage in any of the stages examined. It also differs in its fusion with Meckel's cartilage, in its failure to become completely separated from the extracolumella, and in its degenerate and functionless condition in the adult.

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NOTE ON A RIGHT LUNG WHICH RESEMBLED A LEFT LUNG IN PRESENTING ONLY APICAL AND BASAL LOBES

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During the routine dissection of the thorax of an aged female subject it was observed that the right lung did not present a middle or anterior lobe but that the great oblique fissure which was well defined separated an upper or apical lobe from a lower or basal lobe, thus giving a close resemblance to the left lung. There were no traces of pleuritic adhesions in either lung, nor any signs of the transverse fissure having been obliterated. The general arrangement of the objects comprising the root of the right lung was normal and the right bronchus gave off the ep-arterial bronchus as its first collateral branch. From this circumstance it was deduced that the right apical lobe occupied its customary place. On the other hand, the right hyp-arterial bronchus which was of normal

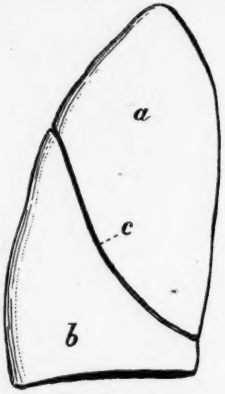

Fig. 1. Right Lung front view.
a, apical lobe; *b*, basal lobe;
c, oblique fissure.

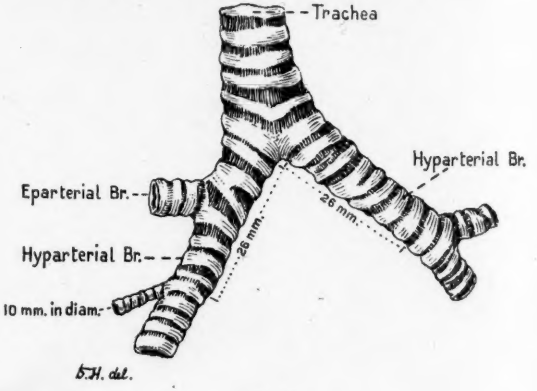

Fig. 2.

dimensions, entered the basal lobe, but just before doing so it gave off about 26 mm. from the bifurcation of the trachea, a quite small branch which entered a piece of lung adherent to and blended with the under side of the apical lobe. The diameter of the lumen of this branch was 6 mm. and this piece of lung was situated deep in the oblique fissure close to the root so that it did not appear as a separate piece of lung tissue either on the costal or

mediastinal aspects of the lung. The left bronchus also began to divide at a distance of 26 mm. from the bifurcation of the trachea.

Assuming that the first branch of the right hyp-arterial bronchus is distributed to the right middle lobe, then the tissue which corresponds to the right middle lobe was really present but much reduced in size and closely adherent to the apical lobe through the non-development of a transverse fissure.

This condition can be accounted for by an early arrest in the growth of the primitive bud from which the middle lobe springs and the consequent non-formation of the transverse fissure, with adhesion of the stunted middle lobe to the larger apical lobe. Further, the condition is of interest as affording evidence that the apical and basal lobes of the left lung correspond with the middle and basal lobes of the right lung since all these lobes are associated with bronchi derived from the hyp-arterial bronchus whereas the right apical lobe belongs to the special ep-arterial branch of the right bronchus.

I have not been able to find a record of the complete absence of a right middle lobe, or, as in the present case, such a reduction in size and adherence to the apical lobe as to suggest its absence and moreover in a long experience I have not seen anything similar and for all these reasons the condition seemed worth recording.

MODERN BRITISH PELVES IN THE "ALFRED HUGHES" MUSEUM OF ANATOMY, UNIVERSITY COLLEGE, CARDIFF

By DAVID HEPBURN, C.M.G., M.D.
Professor of Anatomy, University of Wales

The collection of modern British Pelves which forms the subject of the following comments has been in process of formation for over twenty years, and at the present time consists of fifty-two specimens of which forty-one are male and eleven are female. It therefore seemed to me an appropriate occasion for a review of some of the points of interest arising from a survey of the whole of the collection. I am in a position to guarantee the authenticity of each specimen, since all of them have been collected, prepared and mounted for exhibition under my own supervision, and they are all adult specimens. Differences in detail due to variations in general muscularity are no more frequent than one is accustomed to find among other parts of different skeletons, but in two of the pelves, one a male (no. 41) and the other a female (no. 55), the sacrum consisted of six segments. The additional segment in each case was added to the lower end of the sacrum with the result that both of these sacra presented five pairs of anterior, and five pairs of posterior sacral foramina.

In deciding the nature of this additional segment, two points arise for determination, viz. (1) is it merely the first segment of the coccyx welded or ossified to the fifth segment of the sacrum? and (2) what appearances characterise and determine the first segment of the coccyx?

Text-books generally assume that an additional segment occurring at the lower end of the sacrum is of necessity merely the first coccygeal segment fused to the sacrum, with or without the formation of a complete pair of anterior sacral foramina. No doubt as a general rule this view may be accepted, although it is still necessary to determine the features which characterise the first segment of the coccyx. The distinctive characters of the first coccygeal segment are its cornua which arise from its dorsal and upper aspect and ascend to be connected with the sacrum either by ligaments or by ossification of these ligaments. To me it seems important to observe that cornua are not described as characters of any segment of the coccyx other than the first, and I desire to emphasise these points because in the abnormal sacra to which I am referring, there is in each of them a coccygeal segment presenting cornua but it is situated below the sixth fused segment of the sacrum. If therefore the sacrum is merely augmented by a coccygeal segment, then the second segment

of the coccyx also presents cornua, and this is a possibility which has not hitherto come under my notice. Certainly an additional sacral segment, added to its lower end, whatever its source of origin may be, will not interfere with or materially modify the arrangement of the surrounding soft parts, but a lengthened female sacrum might cause difficulties in labour. In my opinion the two pelves under consideration possess a sixth segment and in neither case is this borrowed from the coccyx.

Pelvic or Brim Index

The pelves were measured in order to ascertain their Brim Index which as is well known provides a satisfactory means of race classification. It is sufficient to state that this index is obtained from the following formula:

$$\frac{\text{Conjugate diameter at brim} \times 100}{\text{Greatest transverse diameter at brim}} = \text{pelvic or brim index.}$$

The indices thus obtained are classified as follows:

Dolichopellic	...	...	above 95
Mesatipellic	...	...	90–95
Platypellic	...	...	below 90

The forty-one male pelves were measured by themselves and the eleven female pelves by themselves, because on account of its adaptation to special functions the pelvis of the female does not adhere to the characters of its race as determined by male measurements. Among the males, the lowest index obtained was 62 and the highest was 99·1 (no. 35), while the average for the group was 76·6. Two other pelves in this group recorded indices of 88·5. With the single exception of "Pelvis no. 35" all were placed well within the limits of the Platypellic group in which races so far apart as Europeans and Mongolians are classified. But the occurrence of such a high index as 99·1 in pelvis no. 35 was somewhat of a surprise since this pelvis was definitely thereby transferred to the other extreme, i.e. the Dolichopellic group, and accordingly I give its measurements:

$$\frac{\text{Conjugate diam. 115 mm.} \times 100}{\text{Transverse diam. 116 mm.}} = 99{\cdot}1.$$

Although this index places no. 35 well within the Dolichopellic group to which such races as Australian Aboriginals and Bushmen notably belong, and although a Dolichopellic pelvis is not expected among European pelves any more than a Platypellic pelvis would be expected among Australian Aboriginals, yet there is not the smallest doubt that no. 35, which was collected by myself direct from the Practical Anatomy Room eleven years ago, is a European (British) pelvis. The measurements given above indicate that the pelvic brim is almost circular since the two diameters are almost alike. The conjugate diameter of no. 35, viz. 115 mm., is apparently fairly long for an European pelvis, because only one other pelvis (no. 52) presented

a similar conjugate diameter, although seventeen of the pelves had conjugate diameters of 100 mm. or upwards. The shortest conjugate diameter in the collection measured 78 mm. The transverse diameter of no. 35, viz. 116 mm., is a small diameter and only two pelves in the group were less, viz. no. 71, which measured 114 mm., and no. 57, which measured 115 mm., while the widest diameter was 150 mm., no. 48. A young male pelvis had a transverse diameter of 100 mm.

Apparently, therefore, in no. 35 we have a pelvis in which a conjugate diameter unusually long is associated with a transverse diameter unusually short, i.e. narrow, with the result that there is a high brim index and a pelvic inlet which is almost circular. Notwithstanding the high brim index, the transverse diameter is greater than the conjugate. Such an index occurring in a group of authenticated British pelves certainly looks startling, but it only emphasises the fact that while indices are of great use for purposes of classification, a too slavish reliance upon them may lead to serious error. I have not had an opportunity of examining any other collection of British pelves and therefore I cannot say whether extreme variations of the kinds I have noted are frequent, but to me it was an unexpected occurrence to find a male British pelvis with a Dolichopellic index and on that account it appeared worthy of record.

Among pelves in this Museum in addition to the British collection I may refer to that of a male Negro in which the brim index is 93·8, a figure which places the Negro in the Mesatipellic group in which the Negro is usually included.

A male pelvis which was purchased under the statement that it was "Indian" (*sic*) but without any authenticity, yields a brim index of 100·9, so that whatever its origin, it is clearly Dolichopellic. The female pelves of the British group in this collection were also measured for a brim index and although not accepted for the purpose of classification, they are interesting on their own account. The lowest index in this set was 62·2, and the highest 85·4, so that all these female pelves were markedly Platypellic, a grouping which is practically independent of race where female pelves are concerned.

Lastly, the "Hughes Museum" possesses the complete skeletons of several Anthropoid Apes whose sex is not authenticated. Of these the brim index is as follows: Gibbon, 148·8; young Orang (? f.), 155·4; adult Orang, 115; Gorilla, 186·9; Chimpanzee, 165·2; and all of these indices are pronouncedly Dolichopellic, whatever the sex of the individuals.

AN UNUSUAL VARIATION OF THE OMO-HYOID MUSCLE

By J. TAYLOR, Ch.M., M.D.
Lecturer in Regional Anatomy, University College, and
Hon. Asst. Surgeon, Royal Infirmary, Dundee

An unusual variation of the omo-hyoid muscle was seen in the Anatomy Department of University College, Dundee, the subject being that of an elderly male.

The attachment of the anterior belly of the omo-hyoid was threefold.

The main fibres, instead of being inserted into the inferior border of the body of the hyoid bone, were continued on to the lower jaw, parallel to, but medial to the fibres of the anterior belly of the digastric. The digastric fossae

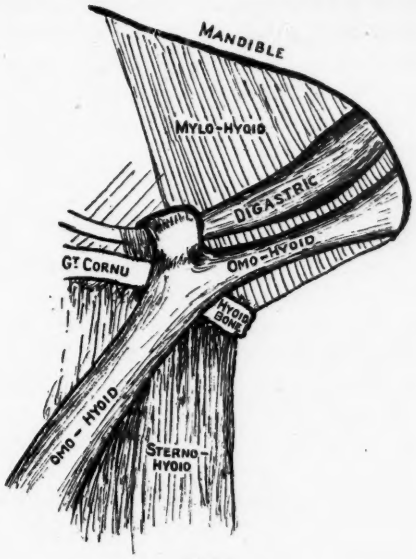

Fig. 1

were more widely separated than usual in order to permit of the omo-hyoid gaining a more medial attachment on the same horizontal level of the mandible. The anterior belly of the digastric, while of normal size, was smaller in bulk than that of the omo-hyoid. The latter had a distinct nerve supply from the nerve to the mylo-hyoid coming off separately from the branch to the digastric.

The second attachment was to the greater cornu of the hyoid bone by means

of a fibro-muscular band which formed a "tacking down" sling for the digastric tendon.

Thirdly, the normal insertion was represented by a very small aponeurotic attachment to the inferior border of the hyoid bone. This attachment was on the deep surface of the muscle. The condition was bilateral and symmetrical.

The writer has failed to discover any previous description of this irregularity, but Testut reports that there are irregularities to be found among the lower animals, and he quotes the Ornithorhyncus whose omo-hyoid sends an expansion as far as the lower jaw (Cuvier and Duvernoy).

Further, in the Caiman, the omo-hyoid divides above into two parts; the more internal part is easily distinguished from the other, and is inserted into the palatine membrane near the jaw (Cuvier and Duvernoy).

Gerard's case reported in *Bibliog. Anat.* (Paris and Nancy), 1899, vol. VII, pp. 269–276 is very exceptional: viz. male subject; 50 years; right side neck; an omo-hyoid arising from the scapula in the usual manner, but having four insertions, viz. to the hyoid bone, sterno-hyoid muscle, sterno-thyroid muscle and the inner end of the clavicle, by a muscular band which curves above and in front of the internal jugular vein and is partly inserted into it.

Testut, in his text-book, details the usual variations, but they are all "infra-hyoid."

IN FURTHER EXPLANATION OF MY THEORY OF THE POLAR AND TRABECULAR CARTILAGES

By EDWARD PHELPS ALLIS Jr.
Menton, France

In a recent article, de Beer makes reference to my work on the polar and trabecular cartilages (Allis, 1923), and after quite fully stating my theory, and practically accepting it in so far as it relates to the polar cartilage and the Selachii, says (1924, p. 332): "But I do not see how the ventral end of the polar cartilage in swinging upwards can pass postero-dorsal to the efferent artery of the arch in the Teleostomes." Several figures are given in illustration, and it is evident, from them, that de Beer has overlooked an all important point in my discussion of the subject; further as it is quite probable that others, also, may overlook it, I am making the present explanation.

The point referred to above relates to the articulation of the pharyngeal element with the epal element in those arches of recent fishes that have assumed the sigma form, and is as follows (Allis, 1923, p. 37): "In the adults of the recent Selachii, where the sigma-shaped arch is found, the dorsal end of the epibranchial in each of the more anterior (branchial) arches is somewhat expanded, the posterior corner of this end giving articulation to the pharyngobranchial, and the anterior corner projecting anteriorly beyond it, as is well shown in certain of Gegenbaur's (1872) figures." It was then assumed that, as the mouth developed, the sigma form was acquired in the mandibular and premandibular arches of the ancestor, or ancestors, of all of the Gnathostomata. In these primitive fishes the efferent artery of the mandibular arch would therefore have lain, primarily, in the hollow of the articular facet on the dorsal end of the epimandibular, between its anterior and posterior corners, these corners later becoming the processus orbitalis quadrati and processus basalis quadrati respectively. The efferent artery of this arch would therefore have lain slightly anterior and ventral to the ventral end of the pharyngomandibular, and I assumed this condition to have persisted in the Teleostomi, for no circulus cephalicus is formed in these fishes. When the pharyngomandibular of these fishes then swung upwards and forwards into a position parallel to the axis of the body, its ventral end naturally passed upwards posterior to the efferent artery of the arch and then forwards dorsal to it, thus leaving the artery ventral to the trabeculo-polar bar, between the orbital and basal processes of the quadrate, in the position it actually has in the recent Teleostomi. In the Plagiostomi, where a circulus cephalicus is formed,

the efferent artery of the mandibular arch is pulled upwards and backwards along the antero-dorsal surface of the pharyngo-mandibular and is lifted upwards when the latter element swings forwards and upwards into a position parallel to the axis of the body; the artery thus here lying dorsal to the trabeculo-polar bar, as is fully explained in my earlier work.

This will, I think, fully explain the conditions in the mandibular arch, as I conceive them, and if I am correct in my conclusion, the dorsal end of the skeletal bar of the arch would be represented in the hinder end of the polar cartilage, and not in either the processus basalis or the processus orbitalis (palato-basal, Gegenbaur) of the quadrate.

In the premandibular arch the relations of the efferent artery to the skeletal bar must have been, primarily, similar to those in the mandibular arch, but as the efferent artery of this arch is the terminal one of the series, its connection with the anterior end of the lateral dorsal aorta (internal carotid) would inevitably have tended to pull it upwards and backwards across the dorso-anterior edge of the pharyngeal element, as the efferent artery of the mandibular arch of the Plagiostomi is so pulled by the formation of a circulus cephalicus. Whenever this occurred, the artery of this arch would be lifted upwards when the pharyngo-premandibular swung upwards and forwards, and this would pull the anterior end of the lateral dorsal aorta (internal carotid) upwards between the hinder ends of the pharyngo-premandibulars, the efferent artery crossing the dorsal edge of the latter cartilage. If the extreme anterior end, only, of the lateral dorsal aorta were thus affected, the artery would run forwards beneath the cranium until it reached the hinder ends of the trabeculae, and would then turn upwards between them, as it does, for example, in Amia (Allis, 1897): but it might be that a considerable part of the anterior end of the aorta would be lifted upwards, in which case the aorta would first pass between the polar cartilages and then upwards between the trabeculae, thus explaining the differences in position of the foramen caroticum in different fishes.

The arteria ophthalmica magna supplies the choroid gland, and arises either directly from the lateral dorsal aorta slightly anterior to the efferent mandibular (pseudobranchial) artery, as in embryos of the trout (Dohrn, 1886), or as a branch of the latter artery. It usually passes dorsal to the trabeculo-polar bar, but certainly not constantly, as de Beer apparently concluded (1924, p. 328), for in Polypterus, for example, where the lateral dorsal aorta does not run upwards between the trabeculo-polar bars (Allis, 1908 *a*), the homologue of the ophthalmica magna evidently cannot pass inwards over the dorsal surface of that cartilage; and the same is probably true also of Amiurus (Allis, 1908 *b*). Wherever this condition occurs, the efferent artery of the arch must have retained its primitive position in the hollow of the articular facet on the dorsal end of the epal element, as the efferent artery of the mandibular arch does in that arch of the Teleostomi, and hence have remained ventral to the pharyngeal element when that element of the arch swung upwards and forwards parallel to the axis of the body.

It therefore seems quite certain that the ophthalmica magna is the efferent artery of the premandibular arch, the choroid gland being probably a derivative of a premandibular gill, as Dohrn long ago suggested. The course of this artery, and the correlated relations of the lateral dorsal aorta to the trabeculo-polar bar, thus both favour my theory of the origin of the trabecular and polar cartilages.

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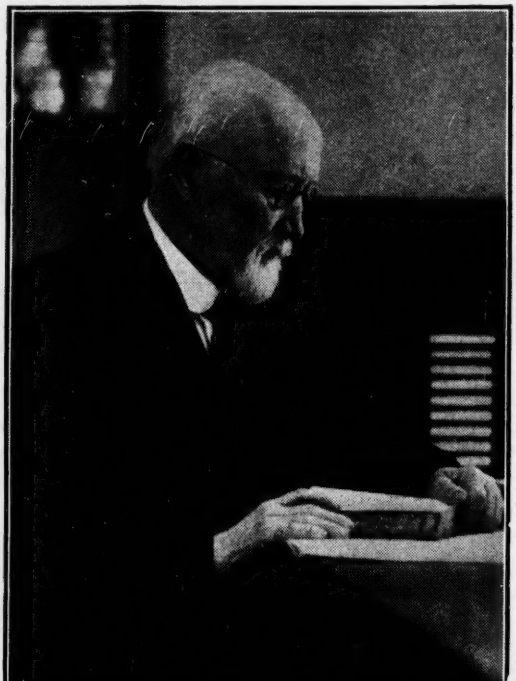
OBITUARY NOTICE

The late Emeritus-Professor NICHOLAS KULCHITSKY.

Histological Science has suffered a heavy loss through the death of our Honorary Member, Professor N. Kulchitsky, on January 30th, as a result of a lift-shaft accident at University College on the morning of the preceding day, which it so chanced was also the 69th anniversary of his birth. At the time of his death, he held the post of Lecturer in Histology in the Department of Anatomy.

Nicholas Kulchitsky was born at Kronstadt in 1856 and in 1874 entered the University of Kharkov in Southern Russia as a medical student. He took



NICHOLAS KULCHITSKY, 1923

his degree with distinction in 1879 and almost immediately joined the teaching staff. Two years later he published his first original papers which dealt with the terminations of the motor nerves in muscle (a subject on which he was

actively at work at the time of his death) and with the origin of the red blood-corpuscles. In 1882 he obtained his M.D. degree for a thesis on the structure of the corpuscles of Grandry. In 1883 he became Privat-Docent, in 1889 Professor-extraordinarius and in 1893 was appointed to the full Professorship of Histology in Kharkov University. He held this post for seventeen years and though invited by the University to continue, he voluntarily retired in 1910, in order that the younger members of his staff might have better prospects of promotion, an act of self-sacrificing consideration for others of which there are but few parallels in academic history.

It is unfortunately impossible to give any adequate account of Kulchitsky's work as Professor at Kharkov. He himself was a most active investigator and published in his own name numerous memoirs ranging over all branches of Histology and histological technique, whilst many papers published by his pupils record work carried out under his direction. Some fourteen of his pupils came to occupy Chairs and other teaching posts in Russian Universities. Amongst his own achievements in Histology may be mentioned his discovery of the presence of three varieties of cells in the cardiac glands of the Mammalian stomach, to the existence of which more than one observer has in recent times redirected attention; his discovery in 1897 of the peculiar cells of the intestinal epithelium now known as Kulchitsky's cells, and regarded by some authorities as the source of secretin; his description of the phagocytic activity of the gastric epithelium in certain fishes; of the emigration of leucocytes through the tonsillar and gut-epithelia and his pioneer contributions to our knowledge of the fertilisation-process in Ascaris.

His profound knowledge of Histology and histological methods is displayed not only in the number and range of his original papers but in his books on Histology and on the Microscope and methods of microscopical research which have long been the standard works on these subjects in the Russian language, and both of which have passed through five editions (1902–1912). He was an expert chemist and devised many new methods in technique of which we need only mention here his fixing fluid, and his modifications of the Weigert-Pal method of haematoxylin staining for medullated nerve-fibres, a method which has been universally adopted and which has made his name familiar to neurologists all over the world.

After his retirement from his Chair, he was not allowed to remain idle and in 1912, at the request of the Government, he accepted the post of Director of Education in Kasan and in 1914 was advanced to the charge of the St Petersburg district. In 1915, his services as Professor and Administrator were recognised by the Czar by the conferment on him of the high honour of the rank of Senator and in the succeeding year, by his appointment to the position of Imperial Minister of Education. He was the last to hold this office, for the revolution followed in 1917. Many of his colleagues suffered the fate of their Imperial Master but Professor Kulchitsky, though thrown into prison, was released after nine days and allowed to return to Kharkov. He lost all his

property and practically all his personal effects and so, to maintain his family, he put his chemical knowledge to practical use and laboured in the Technical Institute of Kharkov at the making of soap, at that time a scarce and expensive commodity. At the latter end of 1918, conditions in Kharkov were such that he decided to go with his family to Sebastopol to the house of his eldest daughter; they were compelled to walk all the way, a terrible journey which took them some twenty-two days. Hardly had they settled down there, when Denekin's army was defeated, and he was fortunate to escape with his wife on board an English ship which took them to Malta. Later on, when Wrangel's troops succeeded in re-occupying the Crimea, they returned to Sebastopol and Professor Kulchitsky once more resumed the making of soap, this time for the Russian Fleet. Finally, when Wrangel's front collapsed in December 1920, he and his wife escaped in an English refugee ship to Bizerta and eventually reached England in April 1921, worn out with their privations and practically destitute.

In the following June, Professor Elliot Smith, learning of Professor Kulchitsky's presence in London, determined with rare foresight to secure his services for his Department and this he was the more readily able to effect seeing that Anatomy was just on the eve of taking over the teaching of Histology from the physiologists. The presence on the staff of an histologist of the ripe experience of Professor Kulchitsky proved of inestimable value in establishing the new Department and possessing as he did an unsurpassed knowledge of technique, his advice and help were constantly sought not only by members of our own staff but also by numerous workers from other institutions. He took an active share, and indeed a very great delight, in the actual teaching work of the Department and more especially in the preparation of the demonstration-material displayed at the meetings of the Histology Class.

His own far-reaching investigations on the innervation of striate muscle, a subject on which he had made his first research in 1881, really arose out of the latter work. In February 1921, Professor Boeke of Utrecht lectured in London on the double innervation of striate muscle and was good enough to give a demonstration of his preparations at University College. This re-aroused interest in the problem and some six months later Professor Kulchitsky set to work to provide demonstration slides and produced a superb series of gold chloride preparations of Python muscle, the study of which resulted in his memoir on "Nerve Endings in Muscles" (*Journ. Anat.* Jan. 1924). In this paper, he demonstrated the presence of two distinct types of nerve-ending in snake's muscle, viz. typical motor end-plates connected with medullated nerve fibres and more diffuse grape-like endings connected with non-medullated fibres, which he regarded as possibly sympathetic. Moreover he showed that the end-plates of the first type are related to muscle-fibres which are always much thicker than those supplied by endings of the second type and that each muscle fibre receives only one type of ending, never both.

It so chanced that the late Professor John Irvine Hunter joined the staff of the Department in 1922 when Professor Kulchitsky was in the midst of this work and it was as the direct outcome of the latter's investigations that Hunter, on his return to Sydney in 1923 initiated in conjunction with Royle, his brilliant researches on the influence of the sympathetic system on "plastic" tone in muscle and devised the operative procedure for the relief of spastic paraplegia. Professor Kulchitsky was present at the meeting of the Anatomical Society on November 28th when Hunter gave a wonderful exposition of the results which he and his fellow-workers had so far obtained and, in common with every one of us, he was most keenly affected by the untimely death of his young friend which followed with such tragic suddenness so soon after.

In October 1924 he published a second paper in this *Journal* on nerve-endings in Frog's muscle, based mainly on the methylene blue technique in the use of which as also of gold chloride and silver nitrate methods he was a past master and on the very evening before his accident, he had completed a third paper on the endings in the muscles of the Lizard, Trachysaurus, and had dedicated it to the memory of John Irvine Hunter. In all his work on nerve-endings, he was extraordinarily cautious in drawing his conclusions, but caution in a problem so exceedingly complex was nothing less than a cardinal virtue. "Young men" he used to say "can afford to make mistakes, they have time to correct them but that is not possible for me." In carrying out his investigations on nerve-endings, he was aided by grants from the Medical Research Council who fully recognised the value of his work.

In addition to being Professor-Emeritus of Kharkov University and a Senator and Privy Councillor of Russia, he was a Commander of the Legion of Honour and a Correspondence Member of the Imperial Academy. He was elected an Honorary Member of our Society in 1923. Notwithstanding the high rank to which he had attained, he was one of the most modest and unassuming of men. Even in the days when he held high office in the Imperial Ministry, it is related that his young son, when questioned by his school-fellows as to the occupation of his father, was only able to reply that he polished violins! Of the latter he had the connoisseur's expert knowledge and in his younger days he was devoted to operatic music. Considering the terrible experiences he had come through, he was wonderfully hale and active for his years and he was very happy in his work at University College. Those of us who have had the great privilege of being associated with him during the last few years only now fully realise how greatly the old man, as we affectionately called him, had endeared himself to every one of us, for he had a very lovable personality and was indeed a very perfect gentleman.

He is survived by his widow, two sons and two daughters to whom we tender our sincere sympathy in the tragic loss they have sustained.

J. P. H.

IN MEMORIAM

JOHN IRVINE HUNTER, M.D.

Challis Professor of Anatomy in the University of Sydney, Australia.

1898–1924

THE untimely death of Professor John Irvine Hunter, briefly announced in the last issue of this *Journal*, was a bitter misfortune not only for his own University, in which he was greatly beloved, but for the science of Anatomy in general and British Anatomy in particular.

To those who knew him well, who looked forward with complete confidence to a career of activity and achievement in keeping with the notable contributions to science that he had already made, his unlooked-for death has brought a sense of irreparable loss.

"For can I doubt who knew thee keen
In intellect, with force and skill
To strive, to fashion, to fulfil—
I doubt not what thou wouldst have been."

Remarkable from many points of view was the life history of this youthful Professor. It is unnecessary here to relate in detail the rather exceptional circumstances of his early life and education. These have been elsewhere admirably set forth with insight and appreciation by Professor Elliot Smith, himself a graduate, though of an earlier period, of the same University of Sydney. It will be sufficient to say that in spite of disadvantages, both physical and economic, which doubtless hampered his early development and concealed his native intellectual powers, and which might have seriously disturbed a less well-balanced temperament, he grew up, not merely normal, but refined and matured by experiences of difficulty and anxiety.

It is not surprising that in his school period the boy did not attain any very special distinction. He was nevertheless successful in gaining bursaries at the High School and University which provided the necessary foothold for further progress.

It was in teaching that Hunter really found himself—in the private tuition which was thrust upon him by the pressure of economic necessity. In this coaching of other students—often his seniors in academic standing—he attained remarkable success through the clearness of his apprehension of the essentials of the subjects he studied and taught and the equally clear and logical order of its presentation to his pupils. But the less settled problems which lie on the fringe of the accepted body of knowledge soon began to occupy his attention. The teacher became the critical enquirer and, when opportunity offered, the first-hand investigator.

Already during the later clinical period of his studies Hunter had undertaken additional duty as a Demonstrator of Anatomy and had revealed unusual capacity for exposition both in the dissecting room and in the lecture room. When, on his graduation, a decision had to be made as between the clinical and the more definitely academic paths of medical science the choice was by no means an easy one. For Hunter had shown a rare aptitude for clinical observation and for the correlation of the data of anatomy and physiology with clinical phenomena. He would undoubtedly have developed into a fine clinician. But he had been powerfully attracted by the interest of various problems of morphology, and the opportunity of devoting himself to their study, combined with his joyful interest in teaching, determined his final choice of a career in Anatomy.

The present writer counts it a privilege to have succeeded in inducing the University of Sydney in 1920 to promote to the Associate chair of Anatomy this youth of 23 who had only taken his degree a few months before. Never was an appointment more completely justified, as was also the proviso made for an early leave-year for the purposes of study overseas for the new Professor.

Owing to the Challis chair becoming vacant soon after Hunter's appointment as Associate Professor, the latter was saddled almost from the outset with the practical responsibility for a large, and then greatly overloaded, department. This involved a heavy burden both of teaching and administration. Hunter not only bore it with apparent ease but lost no time in getting down to research work, not on one investigation but on several.

Before leaving Sydney the writer had handed over to Hunter a specimen of ovarian pregnancy which had been in his possession for several years. Within the year this had been worked up and the results embodied in a paper—his first original paper—which shows a mastery of the relevant literature and conclusively establishes the fact of a true primary ovarian implantation evoking a genuine decidual reaction in the surrounding connective tissue stroma.

Another of Hunter's preoccupations during this inaugural year was an experimental investigation, in conjunction with Mr Royle, at the instigation of Professor Mills, to ascertain the part, if any, played by local vascular disturbance in the production of the symptoms of "spinal shock" in cases of traumatic transverse lesions of the spinal cord. The purely theoretical suggestion had previously been made by the writer that some of the features of so-called spinal shock might be found to depend rather on local vascular disturbance at the site of the lesion than upon mere interruption of conducting tracts. Hunter and Royle's experimental work appears to show that in fact local vascular disturbances at the site of the lesion do play a part in the symptomatology of spinal shock.

This fruitful first year of Hunter's activity produced yet another research in the widely different field of Physical Anthropology. It was carried on in conjunction with his friend and colleague Dr Burkitt and dealt with the

Neanderthaloid characters of the Australian aboriginal skull. A joint paper on this subject was communicated to the Anatomical Society personally and appeared in the issue of this *Journal* for October 1922.

Meanwhile in August 1921 Hunter had set forth on his *Wanderjahr*, which was actually extended to an 18 months' absence from Sydney. Few of those who for the first time encountered this keen ingenuous youth are likely to forget the impression of his personality. For him the period was one of almost feverish interest and breathless receptivity. But by no means of mere receptivity. Both at University College, London, where he had the privileges and opportunities of constant intercourse with its brilliant staff, and for a short period with Professor Ariëns Kappers in Amsterdam, he was busily occupied in actual research along various lines. These included investigations of the structure and relations of the oculo-motor nucleus of Tarsius; the forebrain of Apteryx; and on the problem presented by the Piltdown skull. In addition to all this he found time to carry out a programme of advanced study in various directions and to cultivate relations with other British anatomists and neurologists.

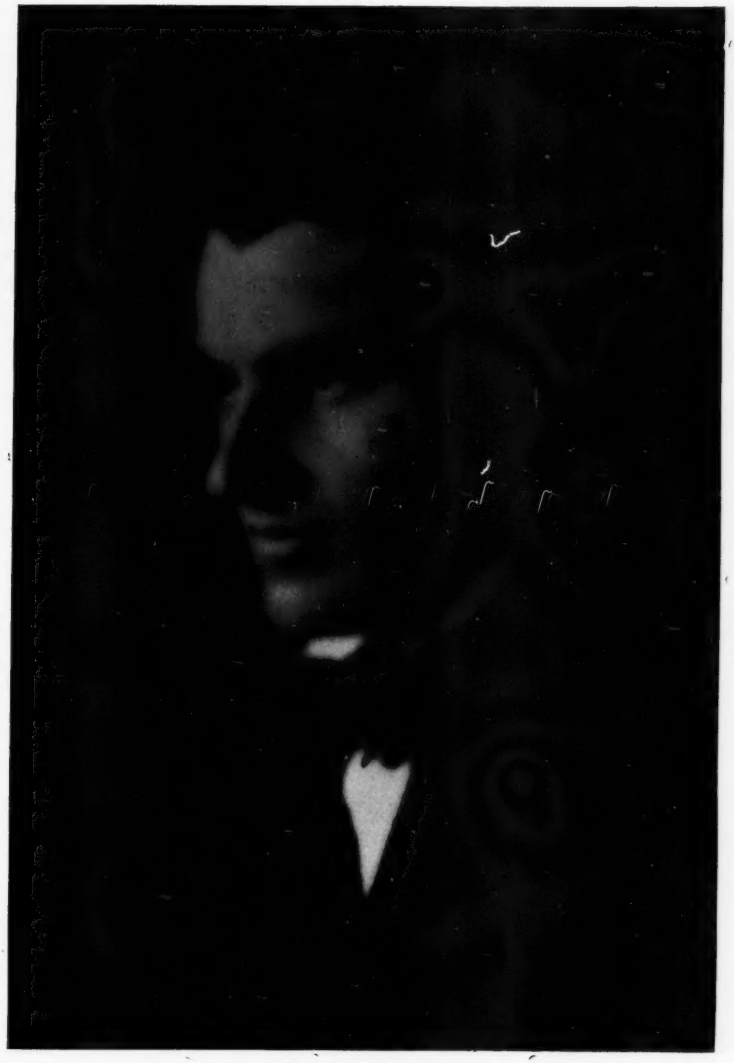
Hunter returned to Sydney early in 1922 by way of America, where he spent two or three months. He was thus enabled to make the acquaintance of a wide circle of colleagues and to familiarise himself with the scope and methods of other schools of anatomy, thus fulfilling to the letter the aim and purpose of this fertile period of travel and enquiry.

Even before his arrival in Sydney the University had itself set the seal of its approval on its young Associate Professor by spontaneously electing him to the vacant Challis Chair of Anatomy which he was destined to hold for little more than two and a half years.

After the *Wanderjahr*, the *Meisterjahre*—so few in number, yet so full of interest and activity, both educational and scientific!

Hunter had now not only to resume the ordinary duties and responsibilities of the full Professorship but he had to undertake the reorganisation of the anatomical teaching on the new basis of the inclusion of microscopical anatomy, so long unnaturally divorced from the study of naked-eye structure. He was enabled successfully to cope with the problems of accommodation and of staffing for the increasingly varied work of his department. In an incredibly short time he had organised his team of assistants and colleagues and had them at work, either on independent research or on some subdivision of the subject which now became his own chief preoccupation, the innervation of muscle.

He had returned to Sydney familiar with the state of the case for the double innervation of striped muscle from his experience in London and Holland and eagerly interested in the questions involved. He found that Mr N. D. Royle, a former demonstrator in the department, with whom he had previously collaborated, was likewise interested in the same problem from the point of view of his orthopaedic practice. He had been struck with



JOHN IRVINE HUNTER

the possible importance of a double innervation of skeletal muscle in regard to the condition of spastic paralysis. Hunter and Royle therefore again joined forces in planning and carrying out an arduous programme of experimental investigation with the view of determining the relationship, if any, of the sympathetic in muscular contraction. This happy conjunction was no merely nominal one but a genuine collaboration, in which each of the partners was indispensable to the other.

As the work progressed it became evident that the workers were on the track of phenomena of far-reaching significance. The issues on the practical side by and by assumed a dramatically striking character when Royle was able to apply them to specific cases in human patients in the new operation of sympathetic ramisection.

This is not the place to attempt an evaluation of either the theoretical or the practical importance of this work of Hunter and Royle. That they have broken new ground by their labours few would now deny. And that the practical application of their work has at least an empirical value in appropriate cases is patent to all who have had the opportunity of witnessing its effects.

Doubtless much work remains to be done in confirming, possibly in modifying, the theoretical explanation of the phenomena themselves. Hunter himself was brimming over with schemes for further investigation. But when criticism and further enquiry have done their work the writer believes that the main result—the establishment of the authentic operation of tonic sympathetic nerve influence upon skeletal muscle—will remain secure. This conviction is based upon the results of certain of the animal experiments which appear to him to be crucial in their character and the conclusion from them inevitable.

Recognition of the practical importance of the work by the surgical world was almost immediate and evidence of this was soon forthcoming in the invitation to Hunter and Royle to deliver the John B. Murphy Oration in New York in October 1924. Hunter's acceptance of the invitation was made possible by the liberality of his University authorities who rightly regarded it as an honour to Australian medical science as well as to the young investigators themselves. They were thus enabled to give lectures and demonstrations not only in New York but in other centres in the United States and Canada.

Hunter decided to return to Australia by way of England and thus had the opportunity on several occasions of expounding his work. And here also, alas! came the tragic end to his brief but brilliant lifework. It is a mournful memory of the writer that it was in his Department in Cambridge that his dear young friend and pupil made his last contribution—lucid and masterly in style—on the subject to which he had devoted the major portion of his short career as an investigator.

No account of Hunter could be adequate which failed to take note of his personal character. A radiant personality, utterly candid and sincere, he

captivated the hearts, as he won the admiration, alike of teachers, colleagues and pupils. His enthusiasm and devotion were infectious and made easy for him the creation of a brotherhood of co-workers fired by his example.

Nor were either his sympathies or his activities circumscribed within the areas of either scientific work or University and educational interests. He was keenly alive to all the varied interests of citizenship. His dutifulness in this regard and his public spirit were conspicuous.

Now this vivid spirit has gone and many hopes in Australia have gone with him. But he has left behind him a memory and an inspiration of priceless value to his University and to Australia. It is in the hope that this inspiration will yet bring forth much fruit that the writer would "reach a hand through time to grasp the far off interest of tears."

J. T. WILSON.

MULTIPLE HYPOGLOSSAL GANGLIA IN THE CALF

By Prof. J. T. WILSON, F.R.S.
Anatomy School, Cambridge

The existence of hypoglossal ganglia and associated dorsal nerve roots in various mammalian groups, especially in embryonic stages, is a well recognised fact. By some observers they have been confused with ganglia of the vago-accessorius system from which, however, they are actually quite distinct.

They often persist, though in relatively reduced condition, into adult life. They appear to be more common in some mammalian groups, like the Artiodactyla and Carnivora, than in others.

The earliest reference to such structures would appear to be a description of them by Mayer (1) in 1833 in the calf, pig and dog and as a rare variation in an adult human subject.

Similar observations were subsequently recorded by others but they seem to have attracted little attention until Froriep (2) in 1882 again recognised the presence of dorsal ganglionated rootlets in the foetal lamb and calf. This observer focused attention upon these structures in connexion with other facts noted by him as bearing upon the segmental constitution of the occipital region in the higher vertebrates. The single well-marked ganglion observed by him as of frequent occurrence has received the name of "Froriep's ganglion."

In 1891 Martin (3) observed in embryos of *Felis* a series of several dorsal hypoglossal roots with ganglia, the more rostrally situated members of which later disappeared.

In 1895, Beck (4), a pupil of Froriep's, made a systematic examination of various mammalian groups with the view of determining, amongst other things, the prevalence among them of dorsal ganglia and roots of the hypoglossal nerve. He discovered a correlation between the occurrence of these and the degree of development of the dorsal roots of the first cervical spinal nerve, which is notoriously variable. He also found dorsal hypoglossal roots and ganglia to be best developed in the Artiodactyla and believed that in them, in some cases, they must possess functional significance.

Since then Lewis (5), Streeter (6), and especially Prentiss (7), have dealt with the embryological side of the problem of the hypoglossal ganglia. The last-named investigator found evidence of the original presence of at least four hypoglossal ganglionic rudiments in pig embryos. In later stages of development it seems rare to find more than one hypoglossal ganglion (Froriep's). Even in the Artiodactyla two were very rarely met with in the later periods.

Langworthy (8) has recently published the results of a study of hypoglossal ganglia and dorsal roots in the cat together with a brief review of the literature

of the subject. In the cat, as also in the dog and rabbit, he found hypoglossal ganglia generally present but exceedingly variable in size and position, often indeed barely recognisable. He never found more than one ganglion in the adult. He proved, however, experimentally that the axons of the ganglionic neurons did actually run peripherally in the hypoglossal nerve but points out that their small numbers and variability negative the view that they are the source of all the sensory fibres to the hypoglossal musculature. He gives a figure of one such ganglion in the cat, showing two fila radicularia and a single small peripheral trunk joining the main trunk of the N. hypoglossus.

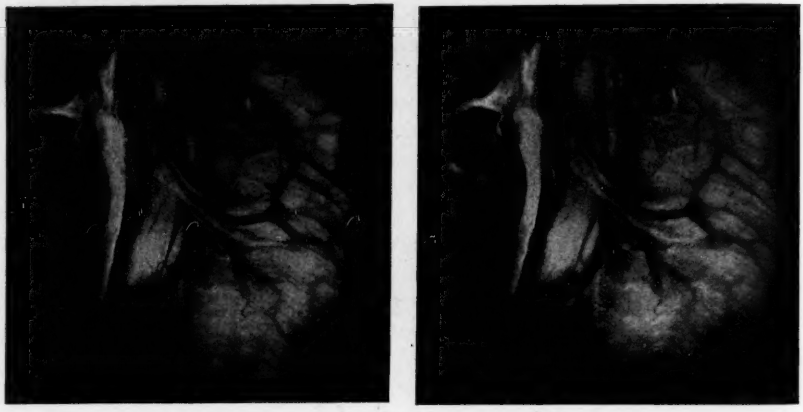


Fig. 1. *Description of stereographic figure, which should be viewed with a stereoscope:* cf. fig. 2 infra.

The figure shows portion of the left side of the medulla oblongata of a new-born calf. Three hypoglossal ganglia come into view on the lateral aspect of the *N. accessorius spinalis*. These give off dorsal nerve roots which are seen wending their way dorsally to enter the dorso-lateral surface of the bulb.

The dense-looking white band lateral to the accessorius trunk is the dura mater which has been slit up lengthwise.

Langworthy concludes that the chief supply of proprioceptive sensory fibres to the hypoglossal musculature must come from other sensory ganglia, cranial or spinal.

In the same No. of the *Journal of Comparative Neurology* in which Langworthy's paper appears, Berkelbach Van der Sprenkel (9) finds that, in *Erinaceus*, sensory fibres run in the peripheral part of the hypoglossal nerve "to enter in greater part the muscles of the tongue." These, however, he found to join the N. hypoglossus via the ramus descendens, their neuronic bodies being situated in the second cervical spinal ganglion. He states that neither sensory fibres nor a ganglion were found elsewhere in the 12th nerve of the hedgehog and remarks that in the Insectivora such ganglia are rare.

In view of the interest aroused by these vestigial structures I desire to

bring under notice an unusually well-marked instance of the occurrence of multiple ganglia with corresponding dorsal rootlets. These were met with on the left side of a new-born calf, where three separate and well-formed ganglia were present. On the right side only one ganglion was present. The accompanying stereogram shows the three ganglia of the left side lying in series alongside of (lateral to) the large spinal trunk of the N. accessorius, to which, however, they are connected only by delicate areolar tissue. From the ganglia fila radicularia may be seen to run dorsally towards the side of the bulb, which they enter in the region corresponding to the funiculus of Rolando.

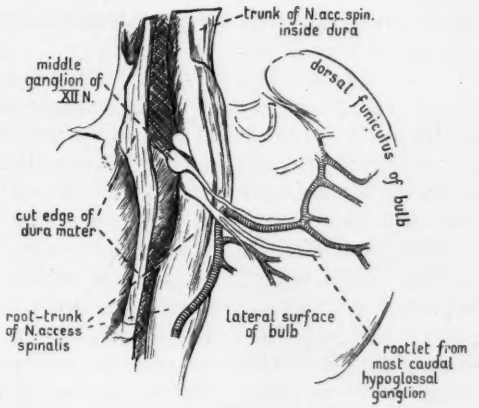

trunk of N.acc.spin. inside dura
middle ganglion of XII N.
dorsal funiculus of bulb
cut edge of dura mater
root-trunk of N.access spinalis
lateral surface of bulb
rootlet from most caudal hypoglossal ganglion

Fig. 2. Key-tracing of stereophotograph of hypoglossal ganglia and dorsal nerve roots in the calf.

On microscopical examination of the serial sections, after Bielschowsky silver impregnation, the root-fibres of these filaments could be followed into the white funicular layer overlying the substantia gelatinosa Rolandi. On entering they were seen to bifurcate, in the manner characteristic of entering axons, into ascending and descending rami. These gave off collaterals, and both the collaterals and some of the bifurcated axons themselves could be traced into the substantia gelatinosa which they entered either directly or after sweeping around the dorsal boundary of the gelatinous area.

These afferent axons of the hypoglossal ganglia, therefore, behaved exactly as do the somatic sensory fibres of the spinal tract of the trigeminal nerve in relation to the substantia gelatinosa Rolandi. Now Ramón y Cajal (10) has shown that a few of the entering root-fibres of the N. vagus (presumably those forming the central axons of those ganglionic neurons whose peripheral fibres constitute Arnold's (somatic) cutaneous branch of that nerve) dissociate themselves from the main stream of afferent (visceral) root-fibres of the N. vagus and plunge into the substantia gelatinosa Rolandi.

In view of these facts one seems warranted in concluding that the gela-

tinous grey matter of Rolando is not to be regarded as a mere appanage, in the way of a single receptor nucleus, of the N. trigeminus but rather as representing a great somatic sensory receptor column of neurons common to any and all of the somatic sensory components of nerves of the brain-stem. If it should prove to be the case, as certain clinical observations in connection with the distribution of herpes in the neighbourhood of the external acustic meatus seem to suggest, that there is actually a minute somatic, general cutaneous, component in the N. facialis, it may be conjectured that the central axons of any such ganglionic elements will likewise find their nuclear receptor neurons in the same gelatinous column of grey matter, just as the *visceral* fibres of that nerve find *their* receptor nucleus in the elongated common visceral column known as the nucleus tractus solitarii.

Berkelbach Van der Sprenkel (*loc. cit.*) cites Weigner as having found the fibres of the intramedullary dorsal root of the hypoglossal nerve running caudally to reach the centre, in the spinal cord, of the dorsal root of the first cervical nerve. A consideration of all the facts would seem to indicate a phylogenetic transference of the main proprioceptive centre for the hypoglossal musculature from an original position in that part of the somatic sensory column known as the substantia gelatinosa Rolandi to a serially homologous position more caudally placed, in the first and second cervical spinal segments.

However that may be, it seems clear, both from the embryonic evidence and from such cases as that just described in the calf, that Froriep was entirely justified in his interpretation of his ganglion as the surviving member of a series of sensory ganglia belonging to the hypoglossal or occipital (spino-occipital) metameres, and that the hypoglossal nerve represents a fused series of three or four segmental nerves. This, indeed, has come to be fairly clear on other grounds, but such cases as that under consideration appear to afford a definite demonstration of the composite character of the nerve in question.

In following out the structural arrangements met with in this connexion, both in the calf and in the cat, where somewhat similar conditions are commonly encountered, I had the advantage, some years ago, of the valued aid of my then assistant, now Professor R. A. Dart, who also later made a thorough and comprehensive analysis of the somewhat extensive literature bearing upon this rather instructive problem.

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THE VISUAL CORTEX OF PRIMATES

By W. E. LE GROS CLARK, F.R.C.S., Eng.

In the course of a systematic study of the brain of the tree-shrew (*Tupaia*) (5), certain features in the structure of the visual area of the cerebral cortex were observed of which the interpretation was somewhat doubtful. In order to seek for an explanation, a comparative investigation of this area was carried out with reference to many brains, primate and non-primate. The results of this study seemed to be sufficiently instructive to warrant their record in the present communication.

In the histological localisation of the cortex of the mammalian cerebrum, the visual area, in the cortex of which the terminal ramifications of the optic radiations are found, is one of the most easily distinguishable of the areas. This has been recognised by most workers in this field who point out that the outstanding characteristic of the visuo-sensory cortex is the well-developed and differentiated lamina granularis interna (Lamina IV)[1]. The most extensive comparative accounts of the microscopic anatomy of this region are those of Mott (9) and Brodmann (2). The results of these two authors are not entirely in agreement, however, either with each other or with the investigations of other authors. This disparity is partly due to the fact that some authors have described as visual cortex what is clearly cortex of quite a different nature. The homologisation of the various cortical areas can be satisfactorily determined only by an elaborate and complete survey of the whole cortex of a large number of specimens, as has been done by Brodmann.

The structure of the mammalian visual cortex in its simplest form is exemplified by the section through the occipital pole of the arboreal marsupial, *Marmosa*, shown in text-fig. 1. In this animal, differentiation of the various layers of the cortex is not very marked, but a definite elaboration of the inner granular layer can be readily seen. The granule cells which compose this layer spread into the pyramidal layer superficially and the lamina ganglionaris on a deeper plane so that the boundaries of the layer are not sharply demarcated.

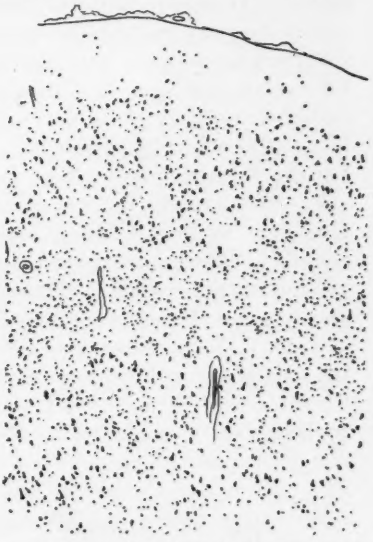
A further differentiation is shown in text-fig. 2 which shows the visual cortex of the rat kangaroo, *Aepyprymnus rufescens*, and this represents the condition which is found in the majority of mammalian brains. The inner granular layer forms a well-defined layer the boundaries of which can be determined fairly accurately, but the granules are somewhat diffusely scattered and, as in the previous case, they merge on either side directly with the cells of the adjacent laminae. A still further degree of differentiation is to be seen in Plate I, fig. 1,

[1] Brodmann's terminology is here used in connection with the cortical lamination.

a microphotograph of the visual cortex of *Macropus brunii*. In this animal the depth of the pyramidal layer is considerable, and the granules are condensed into a narrow and conspicuous band sharply separated from adjacent laminae. The photograph indicates what I have found after a detailed examination of the actual specimens, that the lamina granularis interna consists of a single layer of cells only. Brodmann describes and figures the visual cortex (Area 17 of Brodmann) of *Macropus* as possessing a duplicated granule layer comparable to the condition found in Anthropoidea. I have, however, been unable to confirm this.

The visual cortex of the Anthropoidea, as is well known, possesses a very characteristic structure. The lamina granularis interna is duplicated, being, as

Text-fig. 1. Longitudinal section through the occipital pole of *Marmosa*, showing the visual cortex. The arrow indicates the margin of this area. (Traced with a projectoscope.)

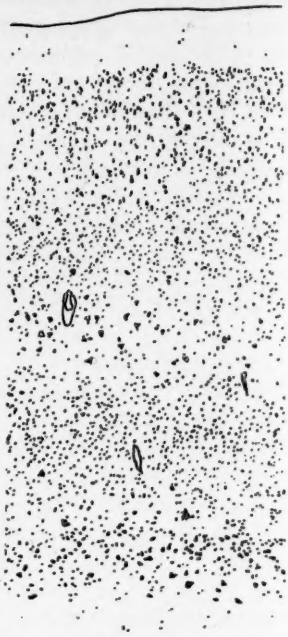


Text-fig. 2. Section through the visual cortex of *Aepyprymnus rufescens*. (Traced with a projectoscope.)

it were, split into two bands by an intervening fibre-layer (the stria of Gennari) in which there are few cells and in which abundant interlacing medullated fibres can be demonstrated by appropriate staining methods. Sections through the visuo-sensory cortex of *Homo*, *Cebus* and *Macacus* have been studied. The latter is shown in text-fig. 3.

An examination of these specimens shows that the two layers of granules are quite well defined. The outer layer (Lam. IV^a) lies close up to the pyramidal layer, the cells of these two layers freely intermingling at their junction. The inner layer (Lam. IV^c) forms a more circumscribed band lying between the stria of Gennari and the lamina ganglionaris. In the pale unstained layer

which lies between them, the stria of Gennari (Lam. IV^b), are to be noted a few scattered cells of the granular type and also some large, relatively poorly stained cells which are similar to the characteristic solitary cells of Meynert also found in the infragranular layers of the visual cortex.



Text-fig. 3. Section through the visuo-sensory cortex of *Macacus*. (Traced with a projectoscope.)

It is interesting to note that Meynert (8) originally described these solitary cells as being present in both these layers, that is, superficial and deep to Lam. IV^c. Thus, in his article "Vom Gehirne der Säugethiere" in Stricker's *Handbuch d. Gewebelehre*, Bd II, 1872, Meynert states: "In diesen zellarmen Gebieten (by which, from the context, he obviously refers to the pallid zones above and below the granular layer corresponding to Brodmann's Lam. IV^c) finden sich einzeln stehend oder in seltenen kleinen Häufchen Pyramiden eines allergrössten, die Ammonshornformation um das Doppelte übertreffenden Calibers (Solitärzellen)." Cajal (3) in his *Histologie du Système Nerveux*, seems to have misinterpreted Meynert's account of the lamination of the visual cortex and describes Meynert's cells as occurring only in Lam. V. He describes large stellate cells in the stria of Gennari which are clearly also the "Solitarzellen" of Meynert. They are similar to those of the deeper layers in possessing well-marked horizontally-directed basal processes. The cells in Lam. V possess more conspicuous apical processes apparently dependent on their deeper situation in the cortex. Most text-books continue to refer Meynert's solitary cells to the lamina ganglionaris. Bolton (1), in his work on the visuo-sensory cortex of the human brain, has recognised this error, for he describes Meynert's cells as occurring in the line of Gennari as well as in the infragranular layer (Layers 3 b and 4 of Bolton).

The presence of these cells of Meynert in Layer IV^b is more marked in the case of *Macacus* and *Cebus* than it is in *Homo*, and in *Cebus* the cells are arranged in an irregular row in the middle of the stria of Gennari which gives the lamina granularis interna of this animal the appearance of being subdivided into no less than five layers, as described by Brodmann.

The characteristics of the visuo-sensory cortex of Anthropoidea may thus be summarised as follows: A duplication of the inner granular layer, the presence of a well-marked stria of Gennari, and the presence of the large and conspicuous cells of Meynert both in the stria and in the subjacent lamina ganglionaris.

The stria of Gennari is present, as shown by various authors, in the visual cortex of most, if not all, mammalian brains, but, except in the Primates and allied forms, it is only clearly visible in sections which have been specially stained to display the fibre tracts. In all Primates, however, the stria is readily seen by the naked eye in fresh unstained brains and in sections stained by cytological methods. Mott has stated that the stria is not evident to the naked eye in the lemur's brain, but Elliot Smith has shown this statement to be incorrect.

Cells similar to Meynert's cells have been described in the infragranular layers of the visual cortex of many mammals, but they appear in their full and conspicuous development especially among Primates, in which they are also found in Lam. IV^{b}.

The origin and significance of the double granular layer found in the anthropoid visual cortex have not yet been settled. It would appear that the two layers of granules have been derived from an original single layer as is shown by the examination of foetal brains, and by the fact that, at the junction between the visuo-sensory and visuo-psychic areas in the adult brain, both layers run together and connect up to form a single lamina granularis interna. Additional light is thrown on the problem by approaching it from the phylogenetic standpoint. Attention may here be drawn to the interesting features of the visual cortex of *Tupaia*. Investigators (5) have of late been emphasising the close relation which this little insectivorous animal bears to Primates and an examination of the brain of the animal will certainly prove instructive.

A microphotograph of the visual cortex of *Tupaia* minor is shown on Plate I, fig. 4.

It will be seen that the pyramidal layer is well developed. At the base of this layer is a pale lamina bounded on its deep aspect by a conspicuous band of granule cells. The pale stria is easily visible to the naked eye in sections stained with toluidin blue and by its presence the extent of the visual cortex can be precisely mapped out without the use of a microscope, for the stria ceases abruptly at the margin of the area. Microscopical examination shows this stria to contain a few scattered cells of the granular type and also some very conspicuous large solitary cells—clearly the cells of Meynert which can also be seen deep to the inner layer of granules. There can be no doubt that this pale stria is the homologue of the stria of Gennari of the Anthropoidea.

The granule layer, however, is apparently confined to the deep aspect of this stria, and in certain regions of the visual cortex this layer displays a very interesting feature. It becomes partially split into two layers by an irregular cleft through the centre. This is shown in the Plate.

On first inspection it may seem doubtful whether this feature bears any significance in relation to the duplicated granular layer found in the Anthropoidea. But a detailed comparison with the visual cortex of *Tarsuis* renders it very probable that it represents actually an incipient form of this duplication.

I am unable to say whether the stria of Gennari is visible in a section of the fresh brain of *Tupaia*, but judging by its distinctiveness in sections stained with toluidin blue and especially in comparison with the visual cortex of *Lemur*, this is almost certainly the case.

A comparison of the visual cortex of *Tupaia* with that of *Lemur* shows a remarkable resemblance. Except that in *Lemur* the cellular content is more rich, the degree of differentiation of the laminae corresponds very closely. My examination of the visual cortex of *Lemur* corroborates the description given previously by Mott and Kelley (10), especially in the fact that there is only one clear layer of granules bounded superficially by a pale stria containing scattered cells of Meynert. Mott and Kelley state that "there is a suggestion of a duplicated line of granules in some scattered cells which lie at the bottom of the pyramidal layer." Granular cells are found interspersed among the deeper pyramids of Lam. III, just as they are found in every layer of the cortex and they may collect together to form fairly obvious localised clumps. But as the figure shows (Plate I, fig. 2), they do not form a definite and continuous band comparable in distinctness with Lam. IV^a of Anthropoidea. On the contrary, the conspicuous band of granules deep to the stria of Gennari shows in places a tendency to split precisely as in *Tupaia*.

The close resemblance of the visual cortex of *Tupaia* to the lemuroid type may be adduced as a strong corroboration of the evidence collected by previous workers to indicate the intimate relation between these two groups of animals.

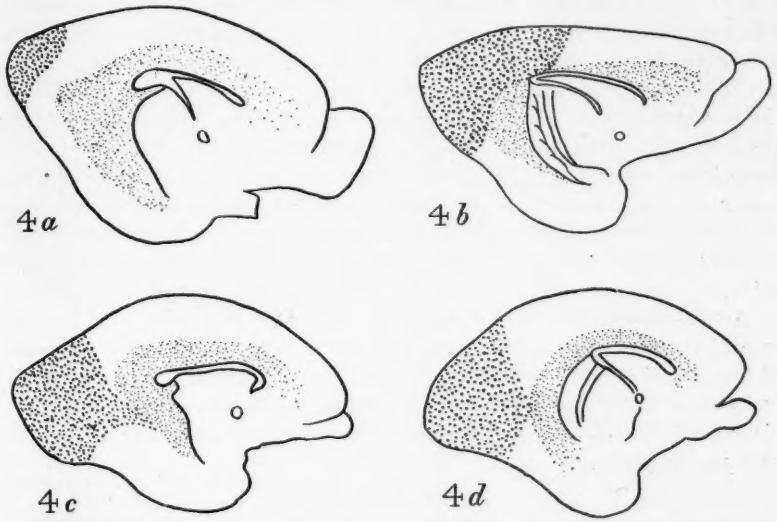
In *Tarsius*, an animal which, in many of its anatomical features, occupies a position intermediate between the Lemuroidea and Anthropoidea, a further (intermediate) phase in the development of the anthropoid type of visual cortex is clearly to be seen. My attention was first called to the interesting structure of the visual cortex of this animal by a study of sections prepared by Dr Woollard whose extensive monograph on *Tarsius* is now in the course of publication, and I would like to express my thanks to him for the facilities which he has given me. I have corroborated his results by sections of one of my own specimens, an illustration of which is shown in Plate I, fig. 5. The microphotograph shows that Lam. IV^a and IV^c have become separated by a distinct and continuous interval. The outer layer of granules, however, does not lie in the position which it occupies in the Anthropoidea—it lies in the middle of the pale stria of Gennari, and is thus separated from the lamina pyramidalis by the outer half of this pale band, in which, as in the stria of Anthropoidea, a few solitary cells of Meynert are to be found. The stria of Gennari in *Tarsius* has been split into two parts by the outer layer of granules.

That these two pale bands both represent parts of the stria of Primates is indicated by their cellular content, their relation to the pyramidal layer, and by the fact that the pale band lying between the two layers of granules is disproportionately small when compared with the stria of allied forms. In

this connection the proportion of the width of the stria of Gennari to the total width of the visual cortex in the following forms may be noted:

Homo $\frac{1}{6{\cdot}6}$, *Macacus* $\frac{1}{6{\cdot}1}$, *Cebus* $\frac{1}{6{\cdot}0}$, *Lemur* $\frac{1}{6{\cdot}9}$, *Tupaia* $\frac{1}{6{\cdot}2}$.

If, in *Tarsius*, the pale stria between the two layers of granules only is regarded as the equivalent of the stria of Gennari, the proportion works out at about $\frac{1}{20}$ or even less. If the interpretation here suggested is adopted, the



Text-fig. 4. Diagrams indicating the extent of the visual area on the mesial surface of the cerebrum in (*a*) *Sciurus* (after Fortuyn); (*b*) *Tupaia minor*; (*c*) *Lemur* (after Brodmann); (*d*) *Tarsius* (after Woollard). (The coarse stipple indicates the visual area and the fine stipple the cingular and associated areas at the pallial margin.)

proportion is found to be about $\frac{1}{6}$, which corresponds to the proportion found in Primates generally.

The structure of the visual cortex in *Tarsius* therefore shows a condition intermediate between that of *Tupaia* and that of the Anthropoidea. It is evident, also, that *Tarsius* is the first representative in the series of Primates which shows a clear and indubitable duplication of the inner granular layer.

A consideration of the evidence afforded by the various types of visual cortex suggests that the structure characteristic of the Anthropoidea has been arrived at by the division of an originally single granular layer lying deep to the stria of Gennari, into two Layers IV^a and IV^c, and the subsequent migration of Lam. IV^a across the stria to take up its position at the base of the pyramidal layer. It is not to be supposed that this process has taken place with the orderly and systematic clearness of a diagram, but that this idea

represents, in the main, the actual course of events in the progressive differentiation of the anthropoid visual cortex seems certain.

Pari passu with the specialisation of the visual cortex of Primates and allied forms, a great expansion of the visual area of the neopallium is to be noted. Elliot Smith has described this expansion in the Primates in detail, and has indicated the part which this process has taken in the formation of the occipital pole and in the production of the calcarine and neighbouring sulci. In this connection it is interesting to note the condition which I have found in *Tupaia* which, so far as available data go, is the most primitive animal which exhibits the primate type of visual cortex. In this animal, the visual area extends to a very considerable distance on the lateral surface of the cerebral hemisphere, and on the medial surface it reaches down actually to the corpus callosum. Such an extension appears to be unique. The cingular areas are thus divided into two parts superficially. Sections taken through the point at which the visual cortex meets the corpus callosum show that the cortex becomes inrolled on the upper surface of the corpus callosum to a distance of 2 mm., thus burying from the surface a strip of cortex which connects the anterior and posterior portions of the cingular regions to each other.

A small but distinct sulcus calcarinus is evident in *Tupaia*, and it would seem that, with the progressive elaboration of the Primate brain, the formation of the calcarine and associated sulci and the production backwards of the occipital pole of the cerebrum provide sufficient surface-area for the expanding visual cortex, so that the peculiar condition found in *Tupaia* may be regarded as a passing phase.

CONCLUSIONS

The following conclusions may be summarised:

1. A clear and indubitable duplication of the lamina granularis interna is to be found only in *Tarsius* and the Anthropoidea.

2. This duplication is foreshadowed in the Lemuroidea and *Tupaia*.

3. A well-marked stria of Gennari which enables the extent of the visual cortical area to be determined macroscopically has been demonstrated only in the Primates and *Tupaia*.

4. In respect of the degree of differentiation of the visual cortex, *Lemur* is paralleled by *Tupaia*.

5. The initial specialisation of the visual cortex is accompanied by a remarkable expansion of its surface area in relation to the rest of the pallium.

6. The structure of the visual cortex of *Tarsius* indicates a position intermediate between that of *Tupaia* on the one hand, and that of the Anthropoidea on the other.

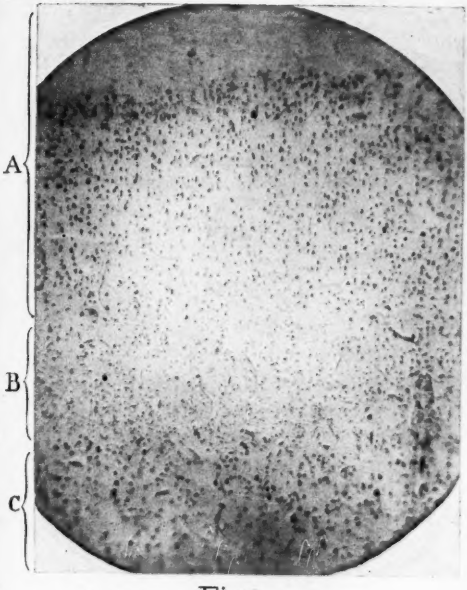


Fig. 1.

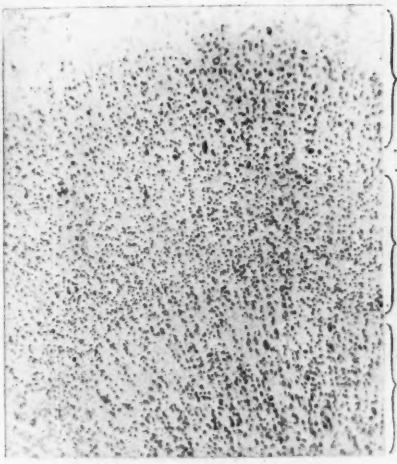


Fig. 2.

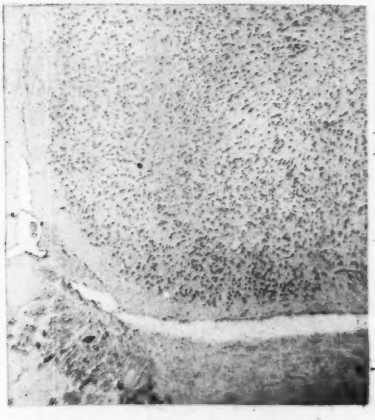


Fig. 3.

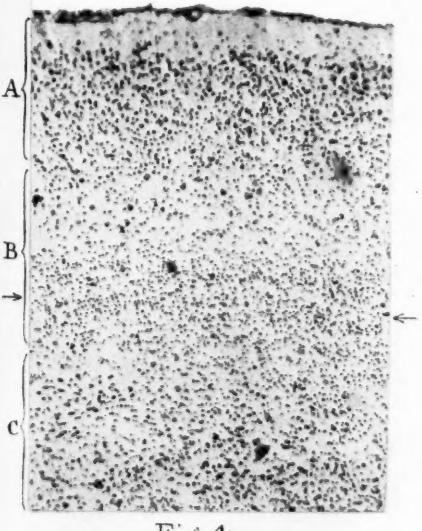


Fig. 4.

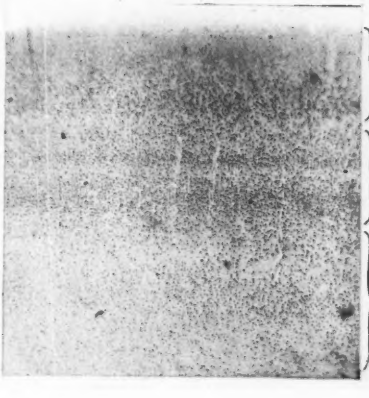


Fig. 5.

DESCRIPTION OF PLATE I

Fig. 1. Microphotograph of a section through the visual cortex of *Macropus brunii*.

Fig. 2. Microphotograph of a section through the visuo-sensory cortex of *Lemur coronatus*.

Fig. 3. Microphotograph of a coronal section through the brain of *Tupaia minor* at the point where the striate area extends down to the corpus callosum. *c.c.* = corpus callosum.

Fig. 4. Microphotograph of a section through the visual cortex of *Tupaia minor* showing the tendency of the inner granular layer to split into two layers separated by an irregular cleft. The latter is marked by arrows.

Fig. 5. Microphotograph of a section through the visuo-sensory cortex of *Tarsius*.

A = Lam. I, II and III.
B = Lam. IV.
C = Lam. V and VI.

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NORMAL AND ABNORMAL NEGROID SEPTA PELLUCIDA

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AND

THE GENESIS OF THE CAVUM SEPTI PELLUCIDI

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A. NORMAL AND ABNORMAL NEGROID SEPTA PELLUCIDA

1. INTRODUCTION

An unusual abnormality of the septum pellucidum discovered during the course of the dissection of a negroid (Zulu) body warranted, in the opinion of the writers, a re-examination of the anatomy and origin of this structure. It was found that the descriptions current concerning this region of the forebrain were for the most part inadequate and the conceptions concerning its arrangement and origin highly conflicting. It was, therefore, felt desirable to preface the description of the abnormal septum with a short account of the types of septum usually found in the negroid races of South Africa.

2. MATERIAL

Among the natives employed in the Witwatersrand area are to be found representatives of nearly all the negroid races which inhabit not only the

Union of South Africa but also Central and East Africa. The result is that the material for investigation is not only considerable but very varied. The septum pellucidum was examined in twelve brains obtained from individuals of the following races: Basuto 3, Zulu 2, Nyambaan 1, Morolong 1, Xosa 2, Shangaan 2, and Pondo 1.

3. THE SEPTUM PELLUCIDUM IN THE NEGROID RACES OF SOUTH AFRICA

(*a*) *The septum as a whole*

The septum pellucidum is the thin vertical partition which intervenes between the anterior parts of the two lateral ventricles of the forebrain in certain mammals. It is attached to the corpus callosum above and to the rostrum of the corpus callosum and the body of the fornix below. It is roughly triangular in shape; the base of the triangle is formed by the rostrum and the sides by the body of the corpus callosum above and the body of the fornix below. The two sides slope backwards to form an acute angle at the apex of the triangle. The base which presents a slight upward convexity extends from the angle at the bend of the genu in front to a point on the upper surface of the anterior commissure behind. It is fairly constant in length, measuring about 1 cm. The upper side of the triangle is formed by the curved under surface of the body of the corpus callosum and extends from the angle at the bend of the genu in front to a point where corpus callosum and fornix meet behind. The lower side of the triangle is the curved upper surface of the body of the fornix; it extends from a point on the dorsum of the anterior commissure in front to that point previously mentioned where it meets the upper side of the triangle posteriorly. In some brains this point corresponds with the point of bifurcation of the body of the fornix posteriorly, but in the majority of cases this relationship does not hold. Where a long septum exists each of its laminae secures an attachment to the crura as well as to the body of the fornix, i.e. the lower side of the triangle is formed in front by the body and behind by the crus of the fornix. This variation in relationship will be referred to again when we come to consider the cavum septi pellucidi.

The angles of the triangle may be described as anterior, posterior and inferior. The anterior angle is the angle formed by the genu and is blunt and rounded; the inferior angle rests on the anterior commissure and is approximately a right angle, while the posterior angle is acute. Obersteiner and Hill name that portion of the septum which passes down to the upper surface of the anterior commissure, i.e. the inferior angle, the pedunculus septi pellucidi. The length of the septum pellucidum as measured along the upper side of the triangle is extremely variable. In twelve negroid brains taken at random, it varied from 2·5 cm. to 4 cm., with an average length of just under 3 cm. The lower side of the triangle is shorter than the upper side and varies according to the length of the latter.

(*b*) *Laminae*

The septum is bilaminar, the two laminae enclosing a space called the cavum septi pellucidi (*O.T.* Vth Ventricle). The laminae are thin, triangular sheets of neuroglial tissue containing a variable amount of grey and white substance. The actual line of attachment of each lamina is from 1 to 2 mm. from the middle line. The laminae slope slightly from above downwards and inwards so that they are slightly further apart at their callosal attachments superiorly than at their fornical attachments inferiorly. The lateral or ventricular surface of each lamina forms a portion of the medial wall of the anterior horn of the lateral ventricle in front and of a variable portion of the central part of that cavity behind. It is covered by ependyma and is bathed by cerebrospinal fluid. The medial surface of the lamina is lined by a thin smooth layer of condensed neuroglial tissue and forms the lateral wall of the cavum septi pellucidi. The thickness of the laminae is very variable. In some brains they are very thin and translucent, in others almost 1 mm. thick and practically opaque. On holding laminae up to the light, we have noticed that not only are there marked differences in different brains, but the individual laminae by no means present a uniform structure throughout. Opaque areas alternate with translucent areas, and running across the lamina are translucent streaks formed by blood-vessels. While there is no absolutely constant arrangement of these areas, one finds that the less translucent areas are massed together along the upper and lower margins of the lamina, while the central strip is usually fairly clear. Further, there appears to be a greater tissue density immediately above and below the veins which show themselves as clear streaks running across the lamina.

(*c*) *Blood-vessels*

Very little information concerning the blood-vessels of the septum pellucidum has been obtained by a perusal of the literature at our disposal. MacAlister states that a small vein is present in each lamina and forms a conspicuous feature in it. The arteries which supply the septum are stated in Gray's *Anatomy* to be the antero-medial ganglionic branches of the anterior cerebral arteries. A number of brains have been injected, the vessels chosen being the anterior cerebral arteries and the great vein of Galen, and it is our intention, at a later date, to give a more comprehensive account of the blood-vessels of the septum. The following preliminary remarks may, however, be made now concerning the veins.

On holding up a lamina to the light, one well-marked vessel, which we may, for convenience sake, term the "inferior vein of the lamina," is clearly visible. It is a large vein which runs horizontally backwards in the lower half of the lamina and is seen more distinctly on its ventricular surface. It begins in the neighbourhood of the genu of the corpus callosum, and, after traversing the lamina, it skirts the lateral surface of the fornix to end at the upper margin of the foramen of Monro in the choroidal vein, near its junction with the ter-

minal vein. It receives numerous tributaries which run backwards along the roof of the anterior horn of the lateral ventricle, bend downwards to descend by way of the lamina and end in the main vein at an acute angle. A few tributaries running in the floor of the anterior horn enter the lamina below and run upwards and backwards to join the main vein.

Another large but less constant vein, the "superior vein of the lamina," runs along the upper border of the lamina. It also is more apparent on the ventricular surface of the lamina. It proceeds backwards between the corpus callosum and the body of the fornix to open into the choroidal vein about an inch from its termination at the foramen of Monro. It receives tributaries from the roof of the lateral ventricle. When the superior vein is absent these last-named vessels descend to join the inferior vein. On the medial surface of the lamina only a few very small vessels are found, and these are present only in certain cases. They run downwards and forwards to enter the main vein of the lamina.

In connection with what has already been stated concerning the increased translucency of the central strips of the laminae examined, it was of interest to find a number of cases in which the areas of the central strip adjacent to the main vein was the most attenuated portion of the whole lamina. This attenuation will be discussed later in detail, as it appears to us to have a distinct bearing upon the abnormal septum to be described later. It is sufficient for our present purpose to indicate that it may point to some tensile process at work in the lamina. The thinning is most marked in these particular cases alongside the relatively fixed line afforded by the main vein.

(*d*) *Minute anatomy*

The minute structure of the lamina of the septum is described in Quain and by Piersol, Obersteiner and Hill and others. In each description there are minor differences which may be accounted for by the fact that there is considerable variation in structure in different laminae. Some are very poorly developed and the different layers indistinctly demarcated. There is, however, a general agreement that there are three main layers:

(1) medially a layer of white fibres,
(2) an intermediate layer of grey matter, and
(3) laterally a layer of white fibres covered with ependyma.

Sections have been cut through a number of laminae, the results of which will be communicated at a later date.

(*e*) *The cavum septi pellucidi*

The cavum septi pellucidi is the median cleft between the two laminae of the septum. It is completely closed in and does not communicate with the true ventricles; further, it is not lined by ependyma and does not possess a choroid plexus. Lastly, it is not formed from any part of the cavity of the

embryonic cerebral vesicles. In other words, the cavum differs very markedly from the true ventricles.

In those brains in which the cavum corresponds in length to the laminae of the septum, its boundaries and relations are the same as those described for the septum. It has a roof, a floor and two sides. The roof is the curved under-surface of the body of the corpus callosum; the floor is formed in front by the upper surface of the rostrum and behind by the arched body of the fornix. Its walls are the laminae of the septum. This state of affairs is, however, exceptional in the negroid brain. In the great majority of cases examined by us *the cavum is longer than the septum* and encroaches posteriorly on the crura of the fornix and the lyra. In the twelve brains previously mentioned the cavum was on an average 1 cm. longer than the septum, the average length being just under 4 cm. In these cases the side walls of the cavum were formed not only by the lamina but also by the medial edges of the crura; and the floor was formed not only by the body of the fornix but by a narrow strip of lyra as well. In one brain, where the cavum was 6 cm. long, it extended back as far as the splenium of the corpus callosum. In this case the lyra or psalterium Davidis formed an extensive lamina stretching across from one crus to the other. It was arranged in the form of a V-shaped trough, the angle of the V resting on the tela choroidea and forming the posterior part of the floor of the cavum. The sides of the V assisted in the formation of the side walls of the cavum.

In those brains which possess a short septum and cavum, a potential space —the subcallosal space—exists between the corpus callosum and the body of the fornix. The attachment of these two structures to each other is not very intimate and the space is easily opened out by a little manipulation. In the great majority of cases the cavum extends backwards into this space, so that the body of the fornix is completely separated from the corpus callosum. In other cases where the cavum is still longer and comes into relationship with the lyra, it encroaches on another space called Verga's ventricle or the ventricle of the fornix. This is the narrow horizontal interval between the corpus callosum and the lyra. It is triangular in shape, the apex being at the point of bifurcation of the fornix, its sides the diverging crura and its base the splenium of the corpus callosum. It will be seen thus that the cavum, in opening out these spaces posteriorly, may have a very variable length. It may, as in the case quoted above, run the whole length of the corpus callosum. What determines its backward prolongation is a matter for conjecture. One may suggest either an increase in the amount of fluid in the cavum or what is perhaps more likely an excessive growth in a backward and lateral direction of the structures which bound the cavum, viz. the crura and the corpus callosum.

The width of the cavum is very variable. In some cases it appears to be merely a potential space—so much so that in opening it the laminae of the septum require to be peeled off each other. In coronal section it shows as a

vertical slit. In other brains it may be as much as 4 mm. wide, forming a narrow rectangle in coronal section. Since the laminae of the septum slope towards each other inferiorly the roof of the cavum is correspondingly wider than the floor. In those cases where the cavum extends as far back as the splenium its roof widens out as the crura of the fornix diverge, so that in coronal section the cavum has a somewhat T-shaped appearance.

Although the width of the cavum is so variable, it is probable that in life the laminae are actually in close apposition with each other and that the space is merely a potential one. This is brought about by the presence on each side of the septum of a varying positive pressure of cerebrospinal fluid.

The cavum is said to contain a small quantity of fluid of the nature of lymph (Quain; Piersol), and is lined by a smooth shining layer of condensed neuroglial tissue which no doubt represents an attempt at the formation of an endothelial lining. The amount of fluid in a cavum 6 cm. long must be appreciable. We have no information, however, as to alterations in quantity or composition of fluid in the cavum in pathological states of the brain.

4. DESCRIPTION OF ABNORMAL SEPTUM PELLUCIDUM

The characters of the abnormal septum pellucidum discovered in the brain of an adult male (Zulu) are unique and bear no resemblance to anything seen in a number of other native brains subsequently examined. Nor is there any record in the literature available to us of a similar specimen.

The principal features are briefly:

(1) The unusual length of the cavum, viz. 6·5 cm. (figs. 1 and 2).

(2) A long septum pellucidum, viz. 5·5 cm. (figs. 1 and 2).

(3) A communication of the cavum septi pellucidi with the right lateral ventricle through a large aperture in the right lamina of the septum (fig. 1).

(4) Two communications of the cavum with the third ventricle (fig. 3).

(5) Abnormal posterior relations of the cavum and an abnormal fornix (fig. 5).

The cavum is an elongated cavity 6·5 cm. long and approximately 1·5 cm. deep running the whole length of the corpus callosum. It may be described as having a roof, a floor and two sides; anteriorly it is closed off by the genu of the corpus callosum and posteriorly by the splenium (see figs. 1 and 2).

The roof of the cavum is an elongated strip of the arched under surface of the body of the corpus callosum. It extends from the bend of the genu to the lower recurved end of the splenium, a distance of 6·5 cm. It is 3 mm. wide in front, 5 mm. at its middle, and 7 mm. wide behind. From it the sides slope downwards and medially to form the floor.

The floor of the cavum is uneven, being roughly concavo-convex from before backwards. It is much narrower than the roof, being formed to a great extent by the coalescence of the two side walls. From before backwards it consists of the upper surface of the rostrum, anterior commissure, body of fornix, lyra and pia mater. The latter, debouching on to the lower end of the splenium,

helps to shut the cavity off posteriorly. It is actually the superior layer of the tela choroidea, which here intervenes between the cavum and the third ventricle.

The floor of the cavum is deficient anteriorly on the right side where it communicates, both in front of and behind the anterior commissure, with the third ventricle. Where in the normal brain the inferior angle of the cavum is formed by the meeting of rostum and fornix on the upper surface of the anterior commissure, in this specimen on the right side these structures fall short of each other and of the commissure—the floor being formed by pia mater and a few strands of white fibres representing the fornix commissure. The rostrum turns abruptly downwards to become continuous with the lamina terminalis. Similarly, the right column of the fornix bends down a short distance behind the commissure and then disappears into the wall of the third ventricle. In this way two narrow passages, a few millimetres wide, are formed leading from the cavum septi pellucidi to the third ventricle. On the left side the floor in this region is normal, the rostrum and left column of the fornix meeting above the anterior commissure.

The walls of the cavum extend from genu to splenium and are formed from before backwards by:

(1) lamina of the septum,
(2) crus of the fornix,
(3) lyra, and
(4) pia mater.

(1) Each lamina of the septum pellucidum is 5·5 cm. long and extend nearly the whole length of the body of the corpus callosum to the under surface of which it is attached. Their inferior attachments are, from before backwards, the upper surface of the rostrum, the bottom of the wide angle between this structure and the column of the fornix, the upper surface of the body of the fornix (which is here less than 1 cm. in length), and finally the crus of the fornix. In front the lamina is 2 cm. high, about its middle 1 cm., while posteriorly it narrows to a point as the crus approaches the under surface of the corpus callosum. As far, therefore, as the shape and attachments of the lamina are concerned, they closely resemble those of the lamina of an unusually large normal septum. There is this important difference, however, that *the right lamina of this septum* (see fig. 1) *possesses a large aperture* through which it communicates with the right lateral ventricle. The aperture is situated about the middle of the lamina, and is an elongated ovoid about 18 mm. long and 6 mm. high. Stretching across the aperture from above downwards and somewhat obliquely are two thin strands which divide it into three compartments, the middle one being the largest. Along the upper and lower margins of the aperture can also be seen two or three small projections, which presumably were points of attachments of similar strands whose central parts have since disappeared. This presumption is strengthened by the observation that the remainder of the margin of the aperture is perfectly smooth and

evenly curved. The left lamina of the septum has the same shape and attachments as the right but does not possess any aperture or other deficiency (*vide* fig. 2).

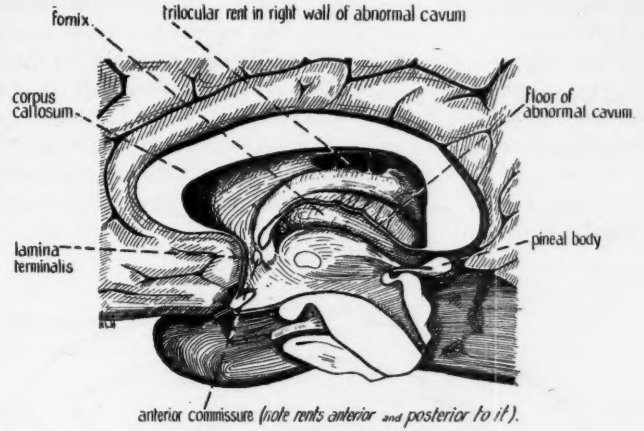
fornix.
trilocular rent in right wall of abnormal cavum
corpus callosum.
floor of abnormal cavum.
lamina terminalis
pineal body
anterior commissure (note rents anterior and posterior to it).

Fig. 1. To illustrate how the abnormal cavum septi pellucidi communicates with the lateral ventricle and with the third ventricle on the right side.

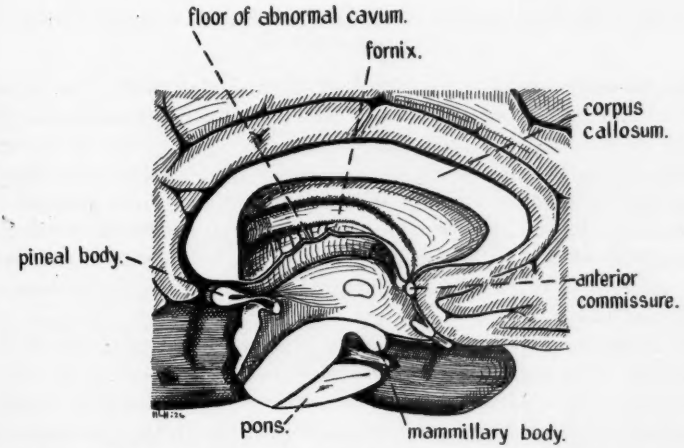

Fig. 2. To illustrate the extent and the relations of the abnormal cavum septi pellucidi on the left side.

On holding these laminae up to the light an interesting state of affairs is revealed. The attenuation which we have found to be a fairly characteristic feature of the normal lamina in the South African negro is apparent here also, but the translucent areas alternate with the thicker opaque areas in a much

more regular fashion. The latter, on the left side, are massed along the upper and lower margins of the lamina and possess processes which, running from opposite sides, meet near the centre of the lamina (*vide* fig. 3). Some of the opposing opaque areas are definitely triangular; the apices of the triangles meet and thus separate the clear spaces from each other. These appearances are significant, for they also afford evidence in our estimation of the method by which the aperture in the right lamina has been formed. It is no presumption to conclude that the attenuation normally present is due to a stretching of the lamina in ontogeny, and it is justifiable to believe that we have witness in these vertically arranged triangular opaque areas, whose apices meet in the central attenuated area, that the forces causing the stretching of the lamina operate vertically to some extent.

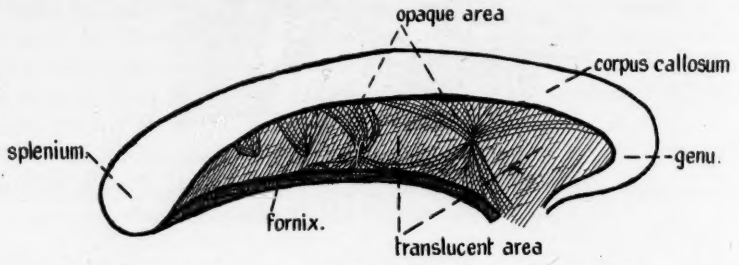

Fig. 3. Diagram of left lamina of the abnormal septum pellucidum as viewed by transmitted light.

The blood-vessels of the laminae are very similar to those in a normal specimen and are also associated with clear areas in their immediate vicinity.

The unusual conditions obtaining in this specimen, where the cavum was undoubtedly bathed in cerebrospinal fluid, provoked a histological investigation of the septal walls. The minutest examination of various portions of the laminae failed to provide any evidence of ependyma or other alteration of the lining of the cavum. It seems, therefore, clear that factors other than the mere presence of cerebrospinal fluid are essential to the production of an ependymal lining.

(2) It has been stated that the crus of the fornix helps in the formation of the wall of the cavum. The body of this structure is about 1 cm. long and is divided into two halves triangular in section connected on their medial and basal aspects by a thin narrow lamina, which helps in the formation of the floor of the cavum. The crura show marked differences from the normal. Anteriorly, instead of being flat they are triangular in cross-section (*vide* fig. 4). Along the upper edge of the crus is attached the lamina of the septum; the mesial wall of the crus forms part of the side wall of the cavum; the lateral wall helps in the formation of the mesial wall of the lateral ventricle, while the base rests on the optic thalamus and is separated from the latter by the tela choroidea. Posteriorly, beyond the septum pellucidum the crura became

semilunar in cross-section, the convex surfaces being medial and the concave lateral (*vide* fig. 5). The former share the formation of the lateral walls of the cavum, the latter in the formation of the mesial walls of the descending horns of the lateral ventricles.

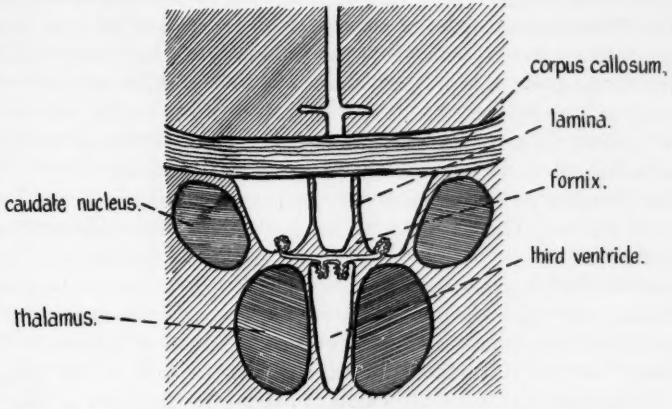

Fig. 4. Schema of a coronal section of the abnormal cavum and surrounding parts anteriorly.

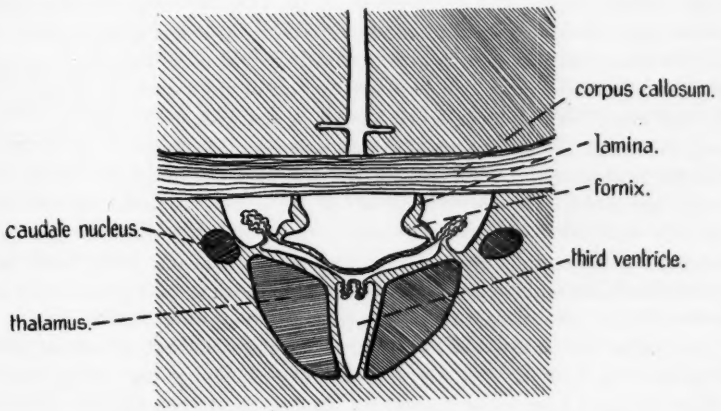

Fig. 5. Schema of a coronal section of the abnormal cavum and surrounding parts posteriorly.

(3) The lyra in this brain is very thin and incomplete. It is deficient posteriorly, the gap between its posterior curved margin and the lower end of the splenium being filled in by pia mater. Running in the lyra and connecting the crura with each other are a few minute strands of commissural fibres of the fornix (see figs. 1 and 2).

(4) The remaining portion of the side wall of the cavum is composed of pia mater which, as we have already stated, forms in the middle line a portion of the floor of the cavum. It is the superior layer of the tela choroidea. Passing forward the two layers dip underneath the lyra and proceed towards the interventricular foramina; laterally they pass upwards over the mesial surface of the optic thalamus and, insinuating themselves underneath the crus, enter the lateral ventricle. Traced backwards the pia mater can be seen to be firmly attached to the lower edge of the splenium and to be continuous with the layer which curves upwards on to the superior surface of the corpus callosum.

The boundaries and relations of the cavum septi pellucidi are best seen in coronal sections taken at different points (*vide* figs. 4 and 5).

There remain to be discussed the pathological aspects, if any, of this abnormal septum. The native, aet. 33, from whose brain the septum was obtained in the course of dissection, died of pneumonia. He had suffered from endocarditis, and vegetations were present on the aortic valves. One of these vegetations must have become separated, for a recent pulmonary infarct was present. There was nothing in the past or present history of the case to suggest a cerebral lesion; nor was there any clinical evidence to make one suspect it. It is conceivable that a minute embolus lodging in the right lamina of the septum might produce necrosis of part of the lamina and, subsequently, an aperture, but the idea is hardly tenable as the rest of the brain was perfectly healthy. Moreover, sections of the lamina in the neighbourhood of the aperture show no signs of old or recent inflammation. For these and other reasons one may also safely exclude such very improbable causes as a ventriculitis associated with ulceration, e.g. tuberculous, new growths, parasites, or an early hydrocephalus. The evidence is all against a pathological cause, and one is forced to accept the condition as either a congenital defect or an acquired developmental anomaly. One cannot but feel that the condition dated from an early age and that the aperture was formed before the fornix and its crura were fully developed. It is conceivable that the entrance into the cavum of cerebrospinal fluid under pressure (as high as 50 mm. and more) must have influenced the size and shape of the cavum and helped to prevent the crowding together of the two crura, which takes place in the normal brain.

This paper was ready to be dispatched for publication when there appeared the interesting note on "A perforated septum pellucidum," published by J. Knox Gibson (*Anatomical Record*, vol. XXVIII, No. 1). As the case described by Gibson is complicated by the presence of a cerebral trauma and insanity, and is the only case known to him and us as being set on record recently, it has still seemed worth while to record the present case.

B. THE GENESIS OF THE CAVUM SEPTI PELLUCIDI

1. INTRODUCTION

Amongst the anatomical pitfalls which embarrass the student may be reckoned the false or fifth ventricle. The very falsity of the *cavum septi pellucidi*, its lack of agreement in type or nature with other brain cavities, and the absence of any satisfactory account of its appearance or reason for its existence have at some time or other puzzled and distressed most of us.

It was, therefore, with an unusual satisfaction that I examined with Dr Beyers a forebrain which seemed to us to afford a very definite clue as to the factors concerned in the ordinary genesis of the cavum as well as in the production of the abnormality it specifically revealed.

In their *Anatomy of the Human Body*, John and Charles Bell relate that the septum pellucidum was discovered by Sylvius and that Sabbatier found it to be of triangular shape and from eighteen to twenty lines in length. They go on to remark, "It has a fluid enhaling into it like the ventricles, and is by some counted as a fifth ventricle. According to Santorini it opens into the base of the brain, opposite to the union of the optic nerves. Vieussens describes it communicating with the third ventricle. Winslow also has seen it reaching a great way backwards and conceives it to open into the third ventricle. Soemmering describes it as large in the middle, contracted backwards, and having no communication; but he asserts that it is shut in on every side. In the base of the brain we find a narrow longitudinal sulcus betwixt the pedunculi of the corpus callosum. In the bottom of this cavity there is a medullary lamina, which Vicq d'Azyr calls 'Cloison à la cavité du septum lucidum,' and the sulcus he calls 'Fosse de la base du septum lucidum.'"

The first item of interest, therefore, which emerges from the specimen here described by Dr Beyers is that it presents a condition of affairs such as was regarded as normal by Santorini, Vieussens and Winslow. It seems highly improbable that a triad of able observers such as these, all of whom enjoy an immortal refulgence at one point or other of the human frame, should have been so completely and independently misled. Perhaps an abnormality of the type they regarded as normal is not so infrequent as many of us may imagine—at any rate this specimen reveals the fact that such an abnormality certainly can and does occur.

A second and greater interest lies in the consideration of the factors concerned in the genesis of the cavum septi pellucidi itself. The specimen illustrates a cavity so enormously expanded as to extend posteriorly between the splenium of the corpus callosum above and the roof of the third ventricle below and to open by a large trilocular foramen into the cavity of the right lateral ventricle at the side and by two small foramina into the third ventricle below. Before we consider the factors concerned in the production of the abnormal cavum, which seem to us to be merely an exaggeration of those concerned in the

production of the normal cavum, it will be valuable to examine the ideas already prevalent upon this subject.

2. DISCUSSION OF THE THEORY PREVALENT CONCERNING THE ORIGIN OF THE CAVUM SEPTI PELLUCIDI

There seems to have been no theory current of the method of formation of this interesting brain cavity, or of the homologies of its constituent walls, in the early part of the nineteenth century, for neither the Bells nor the Monros present any speculations upon the matter. Perhaps no speculation was to be anticipated before the evolutionary principles enunciated by Wallace and Darwin had rendered such hypothesis desirable. However, a conception grew up during the course of the century whose origin, unfortunately, our library facilities do not afford us the opportunity of tracing, but which has become the general teaching concerning the genesis of this forebrain lacuna. This doctrine is perhaps nowhere more explicitly stated than in Gray's *Anatomy* (1923 edition), where we learn that "The cavity of the septum pellucidum is generally believed to be a part of the longitudinal cerebral fissure, which has become shut off by the union of the hemispheres in the formation of the corpus callosum above and the fornix below. Each half of the septum, therefore, forms part of the medial wall of the hemisphere and consists of a medial layer of grey substance derived from that of the cortex, and a lateral layer of white substance continuous with that of the cerebral hemispheres."

This teaching, still current in a standard work of 1923, is to be discovered in one form or another in many of the outstanding textbooks of the Old and New Worlds. Thus Edinger and those authors responsible for the neurological section in such diverse texts as those of Rauber-Kopsch, Quain and Morris, all seem to regard the cavity as formed by the approximation and partial fusion of the cerebral hemispheres. An attempt to unravel the development of the space for the student according to this view is to be found in Morris' *Anatomy*, where the process is depicted as follows: "The corpus callosum, a development of fibres in the upper expanded portion of the lamina terminalis, thus bridges over a portion of the longitudinal fissure between the hemispheres. In the meantime, the fornix arises as two bundles of fibres, one from the hippocampus of each side. In the complex mechanics of the development of the cerebrum these two bundles approach each other under the corpus callosum, fuse for a certain distance, and together arch the cavity of the third ventricle and come to acquire their adult position. There results from these processes of growth a completely enclosed space, a portion of the longitudinal fissure, the roof of which is the corpus callosum, its floor, the body of the fornix, and its lateral walls, portions of the mesial surface of the two cerebral hemispheres."

In assessing the homologies of any structure there are surely two lines of enquiry available, one the study of the developmental facts or ontogeny, the

other the study of the comparative anatomical facts which may afford clues as to phylogeny. Fortunately, in the case concerning us here both these lines of investigation have already been followed by a number of workers. The ontogenetic history of the human septum pellucidum has been investigated by Marchand (1891, 1909), by Zuckerkandl (1901) and by Goldstein (1903). As Streeter (1912) has pointed out, Zuckerkandl (1901) believed that during the formation of the commissures, "There is an approximation and fusion of a considerable area of the median walls (of the hemispheres) with resorption of the previously interposed mesodermal falx. This forms a 'massa commissuralis' through which the fibres subsequently cross." With this view, however, the other embryologists are in sharp disagreement, for Marchand failed to find any concrescence of the cerebral hemisphere walls but showed instead that until the fourth month of foetal life the septum pellucidum is a single solid homogeneous cellular mass interposed between the two lateral ventricles, but that during the fourth month a cavity appears within the previously solid mass; this cavity enlarges as the septum grows and becomes the ventricle of the septum—the septum now becoming bilaminar for the first time. Goldstein also has pointed out that, so far as the commissures (which, as it were, surround the cavum) are concerned, these are developed entirely within the lamina terminalis, and that the adjacent walls of the hemispheres play no part in the process whatever.

Other anatomists express themselves more cautiously. "The origin of the cavity," says Minot, "is uncertain; it has no connection with any of the brain cavities proper; Professor B. G. Wilder writes me that in man and the anthropoids it is wholly circumscribed by brain tissue; it is much narrower in other mammals, but the pia does not extend into it. Marchand thinks it probably arises as a cleft in the tissue."

In his article upon the nervous system in Cunningham's *Anatomy* Elliot Smith (1922) states: "There is still an element of uncertainty concerning the precise manner in which these changes (i.e. the stretching of the paraterminal body and the formation of the two leaves of the septum pellucidum) are brought about, and especially as to the precise mode of closure of the cavum septi."

The conclusions arrived at by the investigations of Marchand and Goldstein are the more trustworthy in that they entirely corroborate the comparative anatomical data. If Zuckerkandl be correct, and the septum and commissures have grown up by concrescence of the hemispheres, it is extraordinary that the whole commissural (anterior, hippocampal and callosal) system has been laid down within and is entirely surrounded by the olfactory field in all Mammalia including Man. We owe to the researches of Elliot Smith the knowledge that this commissural bed is a homogeneous mass throughout Mammalia and that the bed itself is primarily olfactory in nature. It is a portion of the paraterminal body itself. There is no evidence that the lamina terminalis is bilaminar, but the appearance of a cleft in this homogeneous tissue stratum

would be no biological thaumaturgy provided the forces operating upon it were shown to be adequate.

From the standpoint of comparative anatomy this question of olfactory homogeneity is of paramount importance. By this criterion we know that the septum pellucidum of man is to be homologised with the lamina terminalis of all other vertebrates. If Zuckerkandl's description of commissural development in man were correct this homology would be untenable. It would be untenable because Zuckerkandl states in effect that the commissural system of mammals with a cavum (e.g. Anthropoids) is built up in a new tissue —formed by fusion of the cerebral hemisphere walls—which is not present in mammals (e.g. lowly Eutherial) without a cavum. There is not a tittle of evidence to show that an animal gaining a cavum septi pellucidi has acquired any such tissue for the purpose. The ontogenetic and phylogenetic lines of investigation, therefore, find a common point of meeting in the fact that the septum pellucidum in man is not formed by the concrescence of the two hemisphere walls, but was originally a solid homogeneous mass (the lamina terminalis or paraterminal body) uniting the hemispheres, which single mass later became split into two leaves by an operation of forces hitherto undescribed.

No closer parallel between the evidence of development and comparative anatomy could be found than that afforded by the history of the septum pellucidum. It has been stated that the septum or lamina terminalis is solid during the first three months of human foetal life. This is a foetal condition of affairs repeated by all Mammalia during their embryonic history, whether they possess a corpus callosum or not, but with this difference: the condition of a solid septum is found in man only during early foetal life, while it is permanent throughout life in Monotremata (Prototheria), in Marsupialia (Metatheria) and in many of the Eutheria—e.g. Edentata, Rodentia, Carnivora and Cheiroptera. Thus Piersol (1919) states that "The septum lucidum of man is the rudimentary representation of what in many of the lower (macrosmatic) animals is a much more important tract of cortical substance. In some animals, as for example, the rabbit, cat and dog, the septum is solid, a cleft never appearing in it."

So far as I know the actual range of the occurrence, amongst Eutheria, of a cleft in the septum has not been fully investigated. It appears to be present in the highest members of certain orders (e.g. Primates) and to be absent in the lower members of all orders of Eutheria. The presence or absence of a cavum septi pellucidi cannot, therefore, be of any importance from the standpoint of homologisation of the tissue in which it occurs, for even if one were to doubt the completeness of the homology throughout Mammalia one could never doubt the completeness of the homology within a single order of Mammalia, e.g. Primates. As Streeter states, "The ventricle is only present where there is a large corpus callosum." The origin of the ventricle must, therefore, be, as Marchand appears to have been the first to recognise, merely a cleft within the tissue of the septum.

In view of these facts already ascertained, there need be no question of a closure of the ventricle, since it has been enclosed from the beginning wherever it has occurred amongst Mammalia. Cases such as we have under consideration in this paper are not provoked by a failure of the cavity to close, but by an aggravation of this cleaving or clastic process (which we may term, for convenience, "clasis") to which the cavity originally owed its appearance. The "clasis" has proceeded to such an extent that the ventricle of the septum becomes continuous with the third ventricle immediately below and the lateral ventricle to the right.

That this is a correct interpretation of the ontogenetic and phylogenetic facts is corroborated by the data gleaned by Dr Beyers in his examination of negroid brains and of this particular abnormality. He has shown that in these brains an attenuation of the central strip of the lamina is a regular occurrence, that the lines of operation of vertical forces are evidenced by triangular opaque areas whose apices meet in this central strip, and that this particular anomaly demonstrates the "giving way" of the central strip at certain points while "strands" remain to show the remnants of the vertically placed opaque areas.

Nothing, therefore, can be more misleading in the present state of our knowledge than the teaching current in so many of our textbooks, which is at variance with the data of ontogeny and phylogeny and explains nothing to the inquisitive intelligence.

3. FACTORS ACTUALLY CONCERNED IN THE FORMATION OF THE CAVUM SEPTI PELLUCIDI

It remains that we should examine the factors which may possibly be concerned in this clasis of the septum during foetal and phyletic growth. It has already been suggested that the factors are tensile. Streeter (*loc. cit.*) has said of the lamina terminalis: "It is distended dorsalward and antero-lateralward through the growth of the corpus callosum, the shape of which in turn is determined by the expanding pallium. As a result of this tension there is a new arrangement of its tissue, and in the readjustment a ventricle is formed, the so-called fifth ventricle or cavum septi pellucidi. The ventricle is only present where there is a large corpus callosum."

It is an interesting and significant fact that the presence of a fifth ventricle does not synchronise with the first appearance of the corpus callosum. We have learnt that it may be absent from whole groups of Eutheria, all of whose members possess a corpus callosum. It is only when the corpus callosum becomes highly expanded that the ventricle appears. The actual appearance of the corpus callosum is, therefore, insufficient to call forth the cleft. Furthermore, it is difficult to believe that the expansion of the corpus callosum could in itself give rise to the cleft, for it expands in such a way as to exert traction upon the tissue of the septum pellucidum in a single uniform sense, i.e. in a resultant sagittal plane—upwards, forwards and backwards. Such traction

is not likely to be productive of a bilaminar formation and a vertical cleft. It is a further argument against the corpus callosum as the only provocative element in this transformation that this abnormality of an excessively large cleft is found occurring in a Negro, where one would not anticipate such a preponderant aggrandisement of the callosal structures; and, as Dr Beyers has shown, an enlarged cavum is so frequently to be found in Negroid peoples in this country that one is tempted to regard the character as typical amongst them.

If we consider the physical forces to which the septum pellucidum is exposed during development and especially during the fourth month when the fibre tracts are appearing, it is evident that traction is exerted upon it in a variety of ways. There is the traction of the corpus callosum upwards, forwards and backwards in a resultant sagittal plane already mentioned. There is the traction of the anterior commissure whose resultant is in a coronal plane —whose median position of attachment to the septum signifies the lowest point in the cavum septi pellucidi. Finally, there is the traction exerted by the fornix and its commissure. It is mainly to the nature of this latter traction, in our estimation, that the appearance of a cleft and its different varieties is actually due.

This traction of the fornix or hippocampal apparatus resolves itself naturally into three separate components, two of which are in sagitto-lateral or diagonal planes (i.e. the traction exerted by the fornix itself which is attached at one end by its pillars to the side walls of the third ventricle, and at the other end by its crura to the hippocampal formations in the floors of the lateral ventricles), and the third of which is in a transverse or coronal plane (i.e. the traction of the lyra or commissura fornicis which binds the two halves of the fornix together).

In the lowlier Eutheria where the callosal commissure is small, the commissura fornicis (or hippocampal commissure) is almost of the same or even greater dimensions. With the growth of the corpus callosum, as Elliot Smith has shown, the hippocampal commissure is thrust further and further posteriorly and ventrally by the callosal expansion until ultimately it becomes a thin laminated structure. It dwindles, not only relatively, but actually, especially in microsmatic groups such as the higher Primates.

Now the traction of the fornix apparatus we have seen resolves itself into three components, two of which pull laterally and ventrally away from the upward sagittal pull of corpus callosum, while the third component tends to negative the lateral dragging of the halves of the fornix by approximating them to the middle line posteriorly. These facts may be expressed in diagrammatic form by a coronal section through the septum pellucidum posteriorly in a brain where the hippocampal commissure is well-developed (*vide* fig. 6 *a*). In such a brain the transverse linkage between the two halves of the fornix is so strong that the lateral and downward traction is only evident anteriorly and the cavity of the septum pellucidum is not prolonged far posteriorly.

But in cases where the hippocampal commissure is absent or is relatively undeveloped, the lateral and downward pull is felt at its maximum, the two halves of the fornix are torn widely apart, as in this specimen, causing the floor to open into the third ventricle anteriorly, while the side walls of the cavum septi pellucidi may be strained so greatly that it actually gives way and causes a communication to arise between the cavity and that of the lateral ventricle.

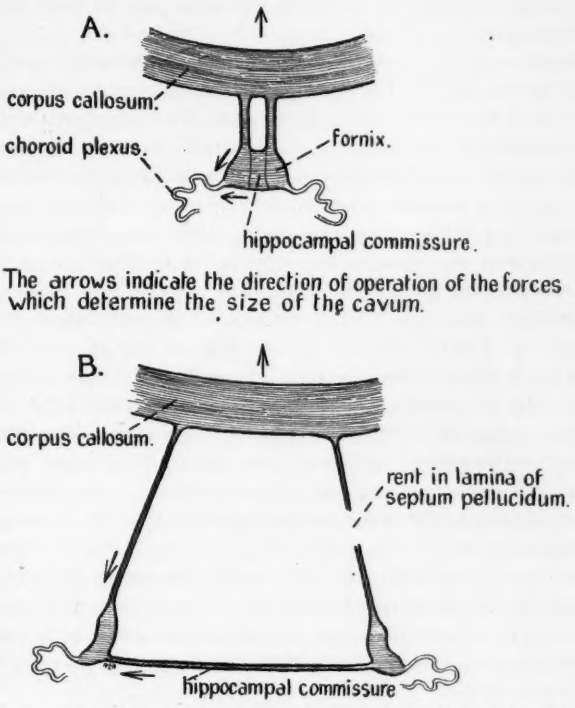

Fig. 6. Diagram to illustrate the consequences of an attenuation of the hippocampal commissure.

The contrasting results of greater attenuation of the hippocampal commissure are depicted in the same diagram (*vide* fig. 6 *b*). This illustrates how the state of affairs obtaining in our present specimen was probably arrived at. The corpus callosum is large but not unduly large, and the fornix on either side is of the usual size, *but the lyra is virtually absent.* A brief examination of the drawing (fig. 1) made from the specimen is sufficient to show that the point at which the right wall of the septum pellucidum gave way was above the apex of the fornix arch—the point at which the maximum effect of the pull was felt. Moreover, the rent was incomplete. Two fine strands of tissue

remained to preserve, as it were, the lines of traction of the two opposing forces of corpus callosum and fornix. In the region of the anterior commissure the lateral divarication was not quite sufficient to separate completely the two halves of the fornix, but their junction at the body was partially severed and slits were formed (between the pillars of the fornix and the anterior commissure behind and between the anterior commissure and the lamina terminalis in front) opening to the third ventricle. Both these openings were more to the right side of the mid-line, i.e. towards the same side as that on which the lamina was broken down.

That the usual appearance of a cavum septi pellucidi is to be attributed to the attenuation of the hippocampal commissure, and the consequently increased ventro-lateral traction of the fornix in animals with a greatly expanded neopallium, seems to us to be corroborated by the fact that the cavity first appears in the fourth month of foetal life when the commissural fibres are beginning sensibly to expand the septum. This fact, coupled with the embryonic and comparative anatomical evidence, confirm the conclusion already stated that there can be no question of concrescence of the cerebral hemisphere walls and subsequent resorption. Since there is no question of concrescence and closure, it is to be anticipated that the origin of the cleft is to be sought in purely physical growth factors operating in the septum pellucidum itself. Of these factors it is evident that the fibre tracts must play a preponderantly important part. It appears equally evident that the tractions of the corpus callosum and of the anterior commissure, important as they may be in affording a basis, as it were, from which other forces might operate in producing the cavity, could not, either of them, in themselves call forth a cavum septi pellucidi. For the production of such a cleft it seems necessary that a laterally operating force is essential, and such a force is normally exerted only by the fornix apparatus and is increasingly apparent with the progressive attenuation of its commissural constituent. It may, therefore, be stated that the fifth ventricle is in the main due to a cleavage or *clasis* in the paraterminal body caused by the ventro-lateral pull of the diagonally running fornix upon the septum pellucidum.

4. CLASIS—A PHENOMENON OF NORMAL AND ABNORMAL GROWTH

In conclusion, this process of cleavage which normally calls forth the septum pellucidum in man is a particular example of a growth phenomenon widespread during development, and for this reason we have given it a specific terminology in the word *clasis*. It is a phenomenon the inverse of that to which Sir Arthur Keith has drawn valuable attention under the term "zygosis." He has shown how during embryonic life innumerable processes of union take place, which are more or less strictly comparable with the phenomenon of adhesion and union in tissues following upon wounds naturally or surgically produced. Under the heading of *clasis* we are in a position to tabulate an

equally numerous series of growth phenomena which are comparable with the changes which take place clinically and surgically when by traction or other interference a partial or complete separation, or even a cavity, is produced. This term *clasis* embraces all the phenomena of cellular or tissue separation, whereas zygosis includes the contrasting phenomena of cellular or tissue union.

The factors underlying *cellular clasis* lead to the phenomena of fission, cell division, cleavage of the ovum and the like. These are gradually being recognised through the labours of many investigators as physico-chemical in nature. The factors underlying the *tissue clasis* of the embryo are less known because they have been less studied. The causes of the appearance of the exto-dermal and entodermal vesicles and the coelome in the embryonic cell-mass —are these physical or chemical or both, at base? The rifts in the tissue masses which provide the pericardial, pleural, and abdominal cavities, the blood spaces, the vacuities between the meninges, the joint cavities, the bursae— what are they? All these phenomena and many others of their type inadequately understood at the present time, present, in the same way as does the resorption of the tail of the tadpole and the laying down of bone in cartilage, examples of tissue clasis. We have in all of these clases which have been of benefit to the organism and have become heritable, inexplicable as their causation and inheritance may be for the present.

In our present abnormality we have a *clasis*, the terminal result of a process of expansion of the cavum septi pellucidi much more common, presumably from Dr Beyer's data, amongst negroid races in this country than amongst Europeans. We are in the presence here of an example of super-development, a mutation whereby at one leap the whole mechanics of the anterior ventricular system of the brain is profoundly altered, and altered in such a way as to be compatible with life and an apparently normal existence. It would be interesting to know if such a condition were actually heritable. If heritable, it is clearly recognisable that still further expansion of the human neopallium is possible, even to the extent of a complete breaking down of the septum pellucidum and the production of extensive forebrain inter-ventricular communication.

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SELF-DIFFERENTIATION IN THE GRAFTED LIMB-BUD OF THE CHICK

By P. D. F. MURRAY (Sydney) and J. S. HUXLEY (Oxford)

The purpose of this paper is to describe two specimens resulting from the grafting on to the chorioallantoic membrane of the chick of fragments of embryonic chick limb-buds.

The first specimen was a very small basal piece of the left posterior limb-bud of a four-day chick. It was grafted on to the chorioallantoic membrane of a chick of seven days' incubation.

On the fourth day of incubation of a normal chick the hind limb is no more than an exaggeration of the Wolffian ridge, consisting of closely aggregated mesoblast cells. On the fifth day the limb-bud consists of a projection from the side with an axis equal to about two-thirds the breadth. A condensation of mesenchyme is beginning axially and proximally, but there has been no cartilage formed. The pelvic girdle develops in continuity with the femur, as two outgrowths of the proximal part of the latter, beginning about the sixth day. About the eighth day the pelvis begins to separate from the femur (Johnson).

The specimen to be discussed was left as a graft for five days. It was then fixed. On opening the egg, the graft was found on the inner side of the chorioallantoic membrane suspended from the latter by a stalk, and having very clearly the general shape of a femur. Its length was about ·75 cm.

Sections showed that the graft now consisted, no longer of a fragment of undifferentiated limb-bud, but of a highly differentiated and very easily recognisable femur.

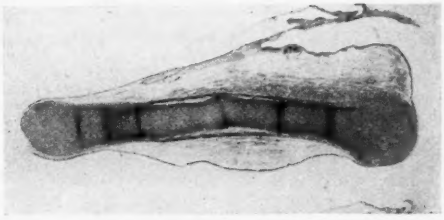

Fig. 1. Longitudinal section of the graft.

Fig. 1 is a photograph of the femur in longitudinal section. The axis consists of well-developed cartilage, more fully differentiated towards the centre, less so at the two ends, where there is less matrix. There are also

more mitotic figures at the ends than in the middle. The central region of the cartilage is surrounded by a double layer of perichondral bone. Fig. 3 shows a high-power view of this bone in process of formation by numerous osteoblasts.

As regards its gross morphology, the specimen is a typical femur. Fig. 2 is drawn from a graphic reconstruction made on squared paper. There is a typical head and trochanter, while the distal end is swollen as though in preparation for the formation of condyles. Situated at the distal end is a small piece of free cartilage in the position of the patella, and there seems to be no reason for doubting that such is its identity, though its shape is somewhat irregular. There is also another small piece of cartilage, to the anterior side of the femur and a little less than one-third the total length of the femur from the proximal end. This probably represents a fragment of displaced pelvis. If so, it is the only piece of pelvis represented in the specimen.

Attached to the right anterior side of the distal end of the femur is some muscle, still in an embryonic condition, and extending to beyond the middle of the femur.

In shape, the cartilage is curved, with the convexity of the curve to the right, just as in the left femur of the adult bird.

It has been said that the specimen was when grafted a very small basal piece of the left posterior limb-bud, and that at this stage the limb-bud is merely an undifferentiated region of mesenchyme cells, with an axial condensation but no more, surrounded by the ectoderm. In the same specimen after five days' life as a graft we find a well-developed femur, both anatomically and histologically highly differentiated, but we do not find any other regions of the limb or limb-skeleton, except a patella and a small piece of cartilage which from its position cannot well represent more distal portions of the limb than the femur, and probably is a fragment of pelvis. Now, if the limb-bud of a chick at four days' incubation were a "harmonious equipotential system," we should expect that a fragment, if it were able to continue differentiation at all, would produce not a femur only, but a whole limb, or would at any rate attempt to do so. The alternative view, that the limb-bud is a mosaic structure, in which the future regions of the limb are predetermined long before they are visibly differentiated, is obviously more in accord with this experiment,

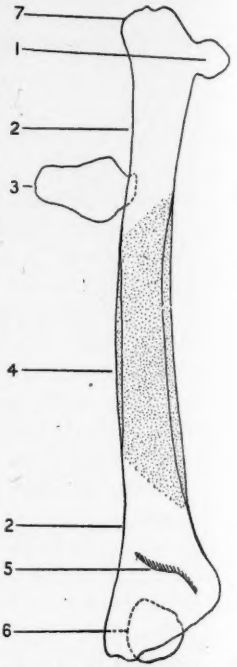

Fig. 2. Graphic reconstruction of grafted femur, viewed from behind.

(1) Head. (2) Shaft of femur. (3) Fragment of ectopic pelvis, on opposite side. (4) Region at middle of femur, ensheathed in perichondral bone. (5) Line of attachment of muscles, on the opposite side of the femur. (6) Patella, on opposite side. (7) Trochanter.

although, until the experiment has been carried out on a larger scale, it cannot be held to be proved. Spurling's experiments, however, in which he extirpated the entire limb-bud, support this view. He was able to show quite definitely that regeneration did not follow upon extirpation of the whole limb-bud, and that after the operation there developed only those parts of the pelvic girdle which had not been removed. Thus the pelvic girdle is certainly a mosaic as regards its various parts; and the entire girdle-complex and appendicular limb form a mosaic as between these two parts, since the girdle Anlagen do not

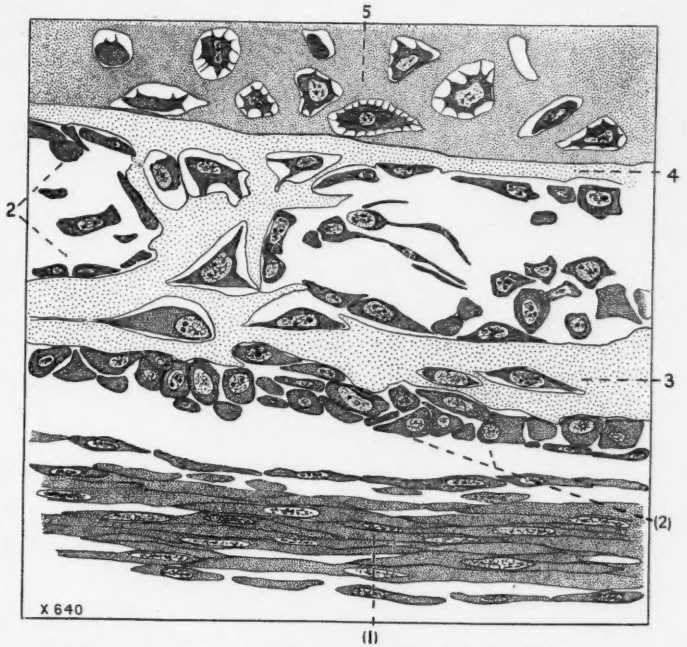

Fig. 3. High power view of perichondral bone of grafted femur.
(1) Periosteum. (2) Osteoblasts. (3) Perichondral bone, outer layer.
(4) Perichondral bone, inner layer. (5) Cartilage.

regenerate the limb axis. But Spurling did not show that the appendicular part of the limb forms a mosaic in itself, because in all his experiments the entire limb-bud was removed. In the experiments which have just been described, however, only a small fragment of the limb-bud was concerned and it only formed part of the limb. It may therefore be provisionally concluded that the limb-bud of the chick of four days' incubation is a mosaic structure in which the potentialities of the various regions are represented spatially, and any region of it is only able to form some or all of that region of the limb for which it was already destined.

It is obviously improbable that the small piece of the limb-bud which was

grafted consisted of the region destined to form femur in its entirety and nothing else. Actually, it is known to be probable that a fragment of the pelvis was included. It is far more probable that either only part of the femur region was included in the graft, and that this part, by regulation, formed an entire femur, or that a small part of the more distal regions of the limb was also included but came to nothing, on account of its small size. Against this latter view is the fact that a small piece of tissue apparently representing a piece of the pelvis was able to differentiate itself to the extent of being able to form cartilage. There seems to be no reason why a small piece of crus should not have done the same thing. Further, it will be seen in Fig. 1 that there is a distinct bend or notch in the femur about the middle of its length, looking as if it had been broken there. This is not seen in Fig. 2 because of course the plane of a graphic reconstruction is at right angles to that of the sections. This bend or notch rather suggests that this may be the point from which the regeneration of the femur proceeded, i.e. that the rudiment of the whole femur region was not included in the graft, but only the rudiment of the part proximal to this notch, the rest having been regenerated. On the other hand, if this were true, one would expect to find a marked difference in the degree of histological differentiation of the two ends of the femur. Such is not the case, both ends being equally differentiated. If this supposition be correct, it is probable that the regenerated end is the distal, since the presence of the piece of cartilage probably representing pelvis would seem to indicate that the proximal end must have been present in the original graft.

This capacity for regulation may at first sight appear to contradict what has been said about the limb's mosaic predetermination. However, if the predetermination is only of whole regions, and fragments of each region can regulate the whole regions, the contradiction disappears. The limb-bud's predetermination is thus not complete in detail, but only in broad outline. It may be called a regional mosaic[1].

This specimen furnishes quite conclusive proof of the ability of the femur to self-differentiate when removed from the proximity of the organs which normally surround it. The question of symmetry hardly comes into this paper, since there can be no question of any influence of the tissues surrounding the limb-bud subsequent to grafting, and we have no information as to what may have happened before grafting. It is important to note that the specimen had its left-handed nature already impressed upon it at the time of grafting.

The work of Peebles should perhaps be mentioned here. She grafted the extremities of fore-limb-buds on to the bases of hind-limb-buds, and *vice versa*, at four days' incubation. She believes that the grafted wing-tip developed as a leg-tip and *vice versa*; but admits that her results were inconclusive. If we accept her view, it would indicate that, even though the limb-buds may be a mosaic structure, yet this is not unchangeable. The work merits repetition. However, Milojević has since repeated the work with regenerating limb-buds

[1] See postscript.

of *Triton cristatus* (young metamorphosed specimens) and finds that Peebles' view is correct, but for the earliest stages of regeneration only. It is not clear, however, from Milojević's preliminary account at what level amputation was carried out. An interesting field for work is here opened up.

Lillie removed the wing-buds of chicks of from three to six days' incubation, and found no case of regeneration.

The second specimen will not be described in detail. Although a certain amount of differentiation has occurred since grafting it has not gone so far as in the previous case, and the form of the specimen is much less regular and more difficult to recognise. It was a piece of either the right or left posterior limb-bud of a four-day chick. The limb-bud of both sides was grafted on to the same membrane, and hence it is not possible, owing to the poor differentiation of the graft, to decide which of the two grafts it is. It was left as a graft for three days only. Histologically it consists of cartilage, still somewhat poorly differentiated, and shading off at the edges into dense mesenchyme (procartilage); this grades again, but in parts with an abrupt transition, into the less condensed mesenchyme of the peripheral tissues of the limb and chorioallantoic membrane. In shape it is very irregular, and it is not possible to recognise particular regions, except that it seems to contain at least a part of the pelvic girdle. The form is too irregular to enable one to say more than this.

SUMMARY

We may conclude from the experiments described that:

(1) The limb-bud of a chick of four days' incubation is a mosaic structure, at least as regards its chief regions, and not a "harmonious equipotential system."

(2) A fragment of the femur-rudiment of a four day chick can undergo regulation and form a complete femur.

(3) Thus the limb-bud at this stage consists of a number of different regions, each predestined to give rise to one segment of the limb only; but each of these regions is totipotent as regards all the parts of the segment to which it is destined to give rise.

It is shown that:

The femur-rudiment of a four day chick can undergo self-differentiation, both anatomical and histological, when grafted on to the chorioallantoic membrane.

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Postscript. Since the above was written, P. Weiss ("Unabhangigkeit der Extremitätenregeneration vom Skelett," *Arch. mikr. Anat. u. Entw. mech.* vol. CIV, p. 359, 1925) has shown that in the regeneration of the limbs of (metamorphosed) *Triton cristatus* each segment of the limb-skeleton will complete itself, but that when a whole bone or set of bones (humerus, shoulder-girdle) is removed entire, they are not replaced; i.e. each segment of the skeleton is toti-potential as regards its own regulation, but the limb-skeleton as a whole is a mosaic of regions with different potentialities. This independently confirms the view we have taken above of the state of affairs in the limb-bud of the four-day chick.

THE INTERNAL EAR OF *OSTEOLEPIS*

By Professor D. M. S. WATSON
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The internal ear is unique amongst sense organs in that its capsule embraces it so closely that the main outlines of its structure and even some of its more intimate details are clearly exhibited by the skeleton.

Although the structure of the semicircular canals of a Palaeoniscid fish was described by Dr Moodie some years ago, no account has yet been given of these structures in the other and even more interesting group of Palaeozoic fish, the Osteolepids.

A specimen of *Osteolepis macrolepidotus* from the Middle Old Red Sandstone of Tynet Burn, Banffshire, in the Museum of the Zoological Department of University College, shows with perfect clearness a cast of the cavities left

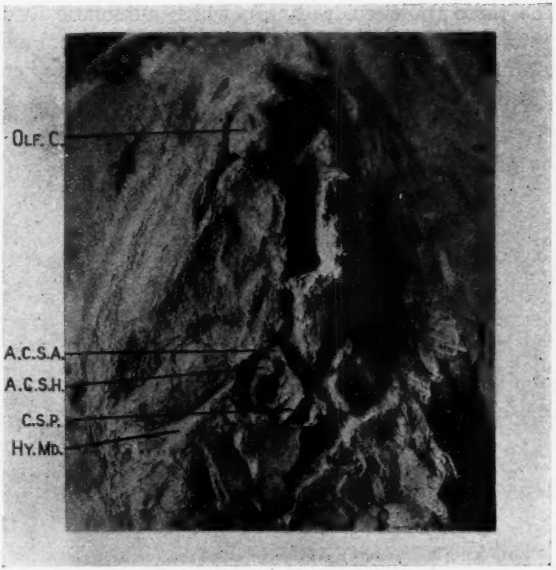


Fig. 1. Head of *Osteolepis macrolepidotus*, × 2 approx.
Olf.C. olfactory capsule; *A.C.S.A.* ampulla of anterior vertical semicircular canal; *A.C.S.H.* ampulla of horizontal canal; *C.S.P.* posterior vertical semicircular canal; *Hy.Md.* Hyomandibular.

in the completely ossified otic capsule of both sides. The specimen is illustrated in the photograph, Fig. 1.

The utriculus opens widely into the brain cavity, and no definite trace of the ductus endolymphaticus is visible.

The anterior vertical canal is longer than the posterior vertical, and rises from the summit of the triangular utriculus, the common vertical canal being extremely short. The anterior canal forms somewhat less than a quadrate of a circle but its ampulla is not markedly bent backward as it is in Palaeoniscids.

The posterior canal forms rather more than a quadrate of a circle with a radius considerably smaller than that of the anterior canal.

The horizontal canal is so bent round as to include rather more than a semicircle, its posterior extremity opening into the utriculus not far behind the common vertical canal.

The ampullae of the anterior vertical and horizontal canals are almost confluent and are connected with the utriculus by a short common duct.

The sacular cavity is not very well exposed but is swollen laterally and shallow dorso-ventrally.

The interest of the specimen lies in its extreme age, it is from the oldest beds which yield bony fish at all, and in the perfectly normal nature of its structure. The three semicircular canals, which automatically analyse any movement into three components referred to rectangular and rectilinear coordinates, form a theoretically perfect mechanism and have hence persisted without any serious modification throughout the vertebrates.

NOTE ON THE OSSIFICATION OF THE SCAPULA

By SYDNEY SMITH, M.D., D.P.H.
Principal Medico-legal Expert, Egyptian Government

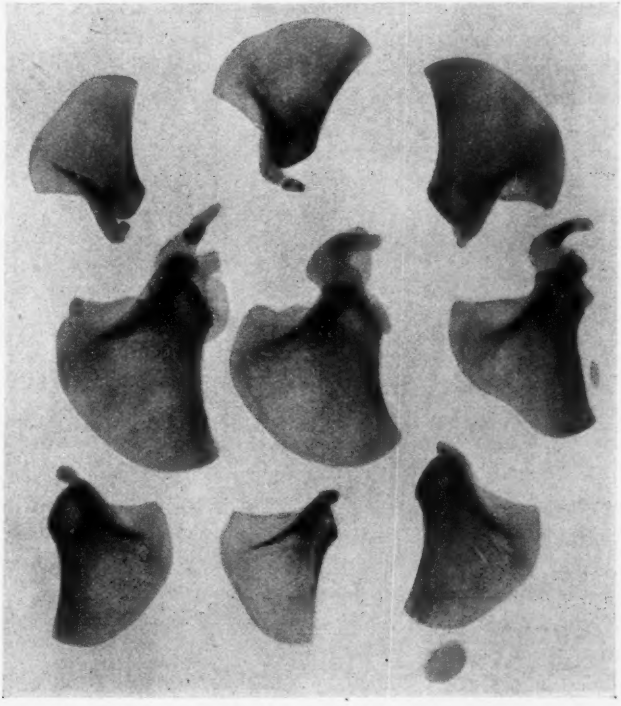
Fifty newly-born infants were recently macerated for the purpose of obtaining a ratio between the body length and the length of the diaphyses of the long bones.

A scapula of a full term foetus was observed in which there was a well formed ossific centre in the cartilage of the coracoid process.

An examination of the whole of the material was made and in eleven cases out of fifty a similar condition was found. The intra uterine age of the infants in which the centre was found was approximately seven and a half months in one, eight to eight and a half in two and full term in the remaining eight.

In a number of the specimens maceration had proceeded to such an extent that the cartilages had completely disappeared and therefore it is probable that the centre was present in a greater proportion than is above indicated.

Cunningham, 2nd ed., vol. I (p. 190), pictures the ossific centre as appearing about the end of the first year, but in view of the above observation this appears to be incorrect. The X-ray plate herewith gives some indication of the size of the epiphysis.



NOTE ON AN ACCESSORY CENTRE OF OSSIFICATION IN THE LOWER JAW

By SYDNEY SMITH, M.D., D.P.H.

Principal Medico-legal Expert, Egyptian Government Service

According to Low, *Journal of Anatomy*, vol. xliv (83), the human mandible is ossified in membrane from one skeletal element on each side and the anterior extremities of Meckel's cartilage do not enter into its formation.

K. von Bardeleben, on the other hand, quoted by the same author, states that the chin in man and mammals has a special skeletal element, the os mentale.

I recently examined a series of about fifty foetal jaws and found that in twelve of them there was evidence of a separate centre of ossification at the symphysis.

The appearance of this varies considerably in the different specimens. In a certain number a distinct ossicle is found attached to each half of the mandible at the lower margin of the symphysis.

In others there appears to be a small process of bone passing across the symphysis from one half of the mandible to the other, and in others there

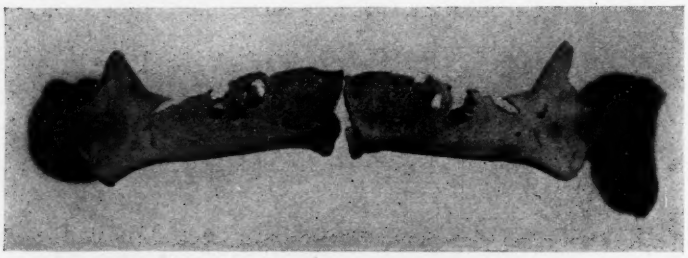


Fig. 1. Mandible of newly born infant showing a well formed ossific centre in the region of the symphysis menti.

appears to be a rounded bar of bone enclosed in the ordinary bone of the jaw on the internal aspect in the position occupied by Meckel's cartilage.

The ossific centre is not observed until about full term, at least I have not noticed it in any premature infant.

Figs. 1 and 2 are photographs of certain of the specimens and give a good idea of the appearance of the centre.

Sections cut through the junction of the two halves of the mandible show one or more cartilaginous nodules in which ossification is taking place.

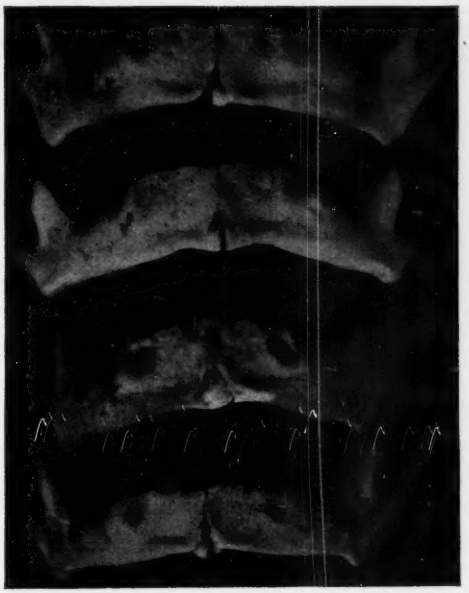


Fig. 2. Four mandibles of newly born infants showing various types of ossific centres in the region of the symphysis menti.

I do not care to hazard any opinion as to whether these ossicles should be considered a definite chin element or whether they are or are not formed from the anterior extremity of Meckel's cartilage, but they occur sufficiently often in the human mandible to be considered a normal feature of this structure.

THE COMPARISON OF AURICULAR HEIGHT DETERMINATIONS

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Hamann Museum, Laboratory of Anatomy, Western Reserve University, Cleveland, Ohio

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INTRODUCTION

It is self-evident that we must have a determination of cranial height and also that the technique adopted should be applicable to the living head as well as to the skull. For this reason auricular height has tended to displace the basion-bregmatic height. The method of estimating auricular height varies very greatly, so that one hesitates to compare measurements made by one observer with those of another. Some workers indeed discard cranial height altogether, especially upon the living, but this is not the best way to escape from dilemma; rather one should endeavour to learn just how far the measurements of different writers may be compared. This latter course is the more necessary since it will be impossible for years to come to persuade all anthropologists to use a single method of determination. Records of heads, lacking determination of height, are of greatly restricted usefulness, for length, breadth and height are associated together in compensating balance.

The Frankfort agreement defines the measurement as the distance, from the upper border of the auditory meatus, of the vertex perpendicularly above it and at right angles (1, p. 67) to the Frankfort plane. With existing instruments, as Martin points out, this may be difficult (2). Many writers therefore substitute the bregma for the vertical point. The Monaco agreement defines this measurement as the distance of the bregma from the porion-porion line (3). English convention adheres to the Frankfort vertical point but measures the distance from the midpoints of the ear-holes (4). On the cranium the bregma can always be found with sufficient accuracy even when all sutures are synostosed but identification of the bregma on the living is sometimes a matter of great difficulty. Anthropologists of experience usually claim to be able to find it invariably but since anthropological measurements are not always taken by workers of considerable experience it would be well to have a stricter definition of the upper limit of the dimension.

Some years ago the Reserve head-spanner was designed to fill the gap in the anthropologist's armamentarium. It is really a Gray's craniometer with the addition of a Frankfort gauge; it has already been described and figured (5, p. 233). The manufacture of this instrument was called for by our own personal needs in this laboratory. We had accustomed ourselves to determining the ear height of crania according to the Frankfort agreement upon a craniostat of Ranke's pattern (6, p. 338) and it became evident that, with the large amount of material at our disposal, we could not afford to neglect the opportunity of comparing the measurement on the cadaver with that upon the cranium of the same individual after dissection and maceration. In order then that the measurement on both occasions should be the same we built the head-spanner with the Frankfort gauge. It has been tested as to accuracy but we still have to learn how far results obtained by its use may be compared with determinations by other workers who have utilised the bregma as the upper limit of the dimension. To this end I have applied myself in the work reported in this paper.

The problem is the comparison of auriculo-bregmatic height with vertical (or auricular) height upon a significant sample of skulls. Skulls are used in place of heads because there is no question, in them, of the identification of the bregma.

METHOD

The procedure has been first, the measurement of vertical height above the porion-porion line when the skull is oriented in the Frankfort plane; secondly, the auriculo-bregmatic height; and thirdly the measurement of the chord distance of the vertical point from the bregma. The skull is mounted in the Reserve craniostat and the auricular height determined. Then the skull supports and the horizontal needle (7, p. 148) are swung out of position and the skull rotated so that the vertex scale touches the bregma, the knife edges of the ear rods remaining in contact with each porion. When the bregmatic prominence is diffuse and the two sides of the coronal suture meet the sagittal suture at different points, the bregma is defined as the point at which the line connecting the two parts of the coronal suture cuts the sagittal suture. The vertical point having been marked upon the cranium the distance between it and the bregma is measured with the sliding callipers (Gleitzirkel).

For this purpose I took one hundred male White skulls without regard to age or character of dentition. This is mentioned specifically because age and condition of maxilla do slightly modify the relation of the Frankfort plane to points near the cranial vertex. The modification is so small that it is negligible in this particular investigation and the sample, being unselected in this regard, approximates more closely to samples with which my results must be compared.

RESULTS

Table I shows that in this series of 100 male White skulls the average auriculo-bregmatic height is 115·2 mm. and the auricular height is 115·1 mm.

The probable errors of the means and the variabilities are identical. This very important result justifies us in comparing directly the cranial height in two

Table I. 100 *male White skulls*

	Mean in mm.	S.D.	C. of V.
Auriculo-bregmatic height	115·2±0·289	4·28±0·204	3·71±0·177
Auricular height (OH)	115·1±0·288	4·27±0·204	3·71±0·177

series when the records of the one series give only auriculo-bregmatic height and the records of the other give only auricular height. For practical purposes it does not matter which method is adopted so long as the sample is one of significant size.

Table II carries the investigation a step further. It shows that, upon the average, the distance of vertical point from bregma is only 11·7 mm. In 92 of our skulls the vertical point lies on the sagittal suture, averaging 12·46 mm.

Table II. *Relation of bregma to vertex*

Bregma-vertex chord: Mean 11·7±0·448, S.D. 6·64±0·317, C. of V. 56·75±3·464	
Number of skulls where bregma lies at vertical point ...	3
Number of skulls where bregma lies in front of vertex ...	92
Number of skulls where bregma lies behind vertex ...	5
Average bregma-vertex distance: above 92 skulls	12·46 mm.
Average bregma-vertex distance: above 5 skulls	4·20 mm.

behind the bregma. In five skulls the vertical point lies on the frontal bone, averaging 4·20 mm. in front of the bregma. In only three skulls do bregma and vertex coincide. This deviation of vertex from bregma is much less than the 2–3 cm. ordinarily given as the distance of the vertex *behind* the bregma. The large variability (56·75 per cent.) indicates however the considerable range in position of vertical point. If we assume that merely stragglers will show a deviation from the bregma of more than three times the standard deviation, we still have a range of nearly 20 mm. in each direction. Hence the range for practical purposes is from about 10 mm. in front of the bregma to rather more than 30 mm. behind the bregma. As the great majority of skulls present a vertex behind the bregma the accepted position of the vertical point is not sufficiently inaccurate to cause any appreciable error. As a matter of fact not one of our series of 100 oversteps these limits.

Table III indicates the effect which is shown in position of the vertical point following infinitesimal alterations in the facial skeleton and Frankfort plane when the dry skull is lying undisturbed on the Museum shelf. I doubt very much if these alterations could be measured directly; they occur in the

Table III. *Alteration in position of vertex in approximately one year*

Skulls completely dried out at commencement of period.

Number of skulls in series	57
No movement	47
Movement backwards	9
Movement forwards	1
Average of 9 above skulls	1·94 mm.
Forward movement in 1 above skull	2·0 mm.

cranial base and the adjacent part of the face but they certainly do appreciably influence the vertical point which lies afar off on the circumference of a circle the radius of which is the auricular height. In the 57 skulls under observation the change takes place in only 10; usually it exhibits its effect in a minute raising of the orbital point of the Frankfort plane with a consequent throwing backwards of the vertex.

The conclusion to be drawn from this work is that we are doing no harm to the cause of physical anthropology in setting forth auricular height on our own large series and in encouraging others to use the head-spanner. On the contrary we are giving confidence in measurement to those who feel diffident concerning their ability always to determine the bregma. In addition we are furthering the prosecution of exact measurement by seeking to substitute a measurement which, with a suitable instrument, can be made definite, for one (auriculo-bregmatic height) which depends largely upon "anatomical appreciation." Macdonell was right in insisting that he must have a fixed point for measurements of height but he was altogether wrong in assuming that the bregma, which he could see, is more definitely a fixed point than the vertex which he could not see (8, pp. 335–6).

SUMMARY

1. For practical purposes it is immaterial whether one use the bregma or the vertical point in measurements of auricular height, provided the sample taken be of significant size.

2. The vertical point has the advantage that it bears a definite relation to the Frankfort plane. Since it is determined automatically by the employment of a suitable instrument it has an advantage over the bregma which, in the living, can be estimated only by anatomical appreciation.

3. The average distance between the bregma and the vertical point in male White skulls is 11·7 mm. but the variability of this deviation indicates that the vertical point may be found anywhere from 10 mm. in front of the bregma to 30 mm. behind the bregma. In the great majority of crania it lies behind the bregma.

4. There may be a small divergence from time to time in the exact position of the vertex on dried skulls following minute adjustments in the cranio-facial skeleton.

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POSITION OF THE ANTERIOR NARES

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INTRODUCTION

The fact that in man the nostrils open downwards, whilst in most other animals the opening is directed forwards, leads to an enquiry as to the cause of this difference.

If a man, a dog, and a horse are observed as they approach, it will be noticed that in the case of the two latter animals, the openings of the nose are visible, but in the first-named instance the nostril is hidden, because it opens downwards. It would make a very great difference if one looked straight into the nasal fossa of fellow beings, but it is a point which does not obtrude itself, because of force of habit. To others the factors concerned are no doubt familiar, but to the writer no clear explanation has been forthcoming from the publications available to him.

To discover the influences governing these differences in inclination, it is best to examine species of lowly type, possessed of an organ comparable to the nose of man.

Fish

Amongst fish, it is found that in the majority of species there is an olfactory organ, consisting in many cases of an anterior and a posterior nostril, united by a passage of varying length and complexity. On the course of this passage is situated an olfactory rosette, in which the terminals of the first nerve are so placed that they can be stimulated by odours dissolved in the water in which the fish lives. Various mechanisms exist to direct a current of water in at the anterior and out at the posterior nostril (1) but it is not intended to study such details in the present paper.

Of fish, three species are illustrated, which show great differences in the position of the nostril in question.

In the case of the John Dory (*Zeus Faber*, fig. 1) it will be seen that the opening of the mouth is situated at the extremity of the snout, and that any food taken in will be visible to the eye. If the fish can see what it is eating, it can tell whether the prospective diet is suitable for its requirements; therefore it does not need any other test of fitness. It has an olfactory organ placed close to the eye, with the anterior nostril at a very short distance only from the orbit, but at a considerable distance from the mouth. The fish does not hunt prey by scent, and merely picks up what stray morsels it can; it is

probably informed by its olfactory organ as to the nature of its environment. Its olfactory sense is probably a general one, and is not directed to particular morsels; consequently no close relation is required between mouth and nose.

The Conger (*Conger vulgaris*, fig. 2), on the other hand, does hunt by scent(2) and is found to have a long olfactory channel, and an anterior nostril placed at the end of a short projecting tube just above the mouth. It can follow the fish it wishes to capture by means of its nose, and is aided to success by the fact that when the nostril is close to the prey, the mouth must be in a position to open and engulf the victim. The John Dory—if it relied on a similar method—would get the intended victim in the eye and not in the mouth.

The Dog fish (*Scyllium canicula*, fig. 3) stands as a type of sharks in general and is essentially predatory. Its mouth has migrated to the ventral surface of the snout and is out of sight of the eyes, which are placed dorsally and towards the middle line. Consequently this fish cannot see what it is eating, but it can, on the other hand, smell whatever is about to enter its mouth because the nostrils are placed ventrally, in close proximity to the oral aperture.

From these observations it would appear that the olfactory organ has the function in some cases of guiding the fish into such a position that the mouth is suitably placed for seizing prey; and secondly, that the near relation of the anterior nostril to the mouth enables the individual to recognise between various foods, and to discriminate between edible and useless or harmful substances.

Illustrations will be given to show to what degree this near relation exists in various species, and in each case a dotted line has been inserted to indicate in which direction a current of inspired air will flow.

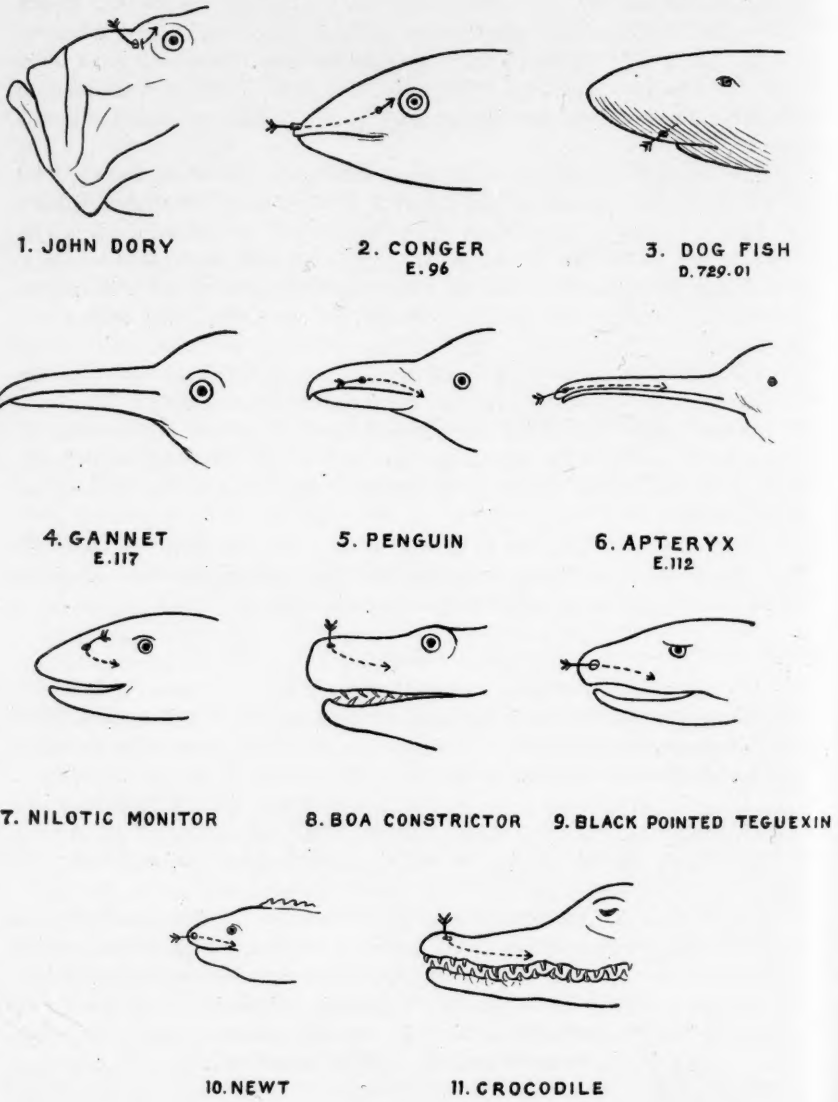
Birds

Amongst birds, it is usual to find that the sense of olfaction is deficient. Particularly is this the case in the order of Steganopodes, to which the Gannet (*Sula bassana*, fig. 4) belongs(3); this bird has no external anterior nostril at all, and is therefore dependent on the eye to warn it of the nature of food. The Penguin (*Spheniscus demersus*, fig. 5) occupies an intermediate position, and although the olfactory bulb is small, nevertheless it is bigger than in most other birds(3). In this species the anterior nostril opens half-way along the beak.

In the Apteryx (*Apteryx Mantelli*, fig. 6) there are big olfactory bulbs and a well-developed sense of smell; the olfactory organ has its anterior opening placed just above the tip of the very big bill. It would appear that this bird would then derive great help in locating and identifying food, and would be enabled to reserve its powers of sight for warning against danger. In a wingless species this arrangement must be of great advantage.

Reptiles and Amphibians

In the suction breathing cold-blooded animals there can be only one reason for the passage of air through the nose, and that is for the maintenance of olfaction; there could be no point in warming the air, nor is there any mechan-



ism of complicated turbinals, or extensive area of mucous membrane, to serve such a purpose. Of such a type is the Boa Constrictor (*Boa constrictor*, fig. 8); air is sucked into the lungs by expansion of the ribs, and can be taken in readily through the mouth. The proximity of the nostril to the mouth must serve a useful purpose in identifying food, although in the process of striking at prey reliance is placed on the eyes.

In animals which breathe entirely or in part by means of a bellows apparatus in the floor of the mouth, the nose is used for passage of air, and in many cases is of a valvular nature. Instances of this type are seen in Newts (*Triton cristatus*, fig. 10) and Crocodiles (*Crocodilus*, fig. 11), in both of which the nostril opens close to the mouth; particularly is this the case in the latter, but the reason is not necessarily an olfactory one, because this particular reptile uses the orifice for respiratory reasons, and is enabled to lie hidden in a river with only the tip of the snout above the surface.

Amongst Lizards, the Nilotic Monitor (*Monitor niloticus*, fig. 7) has a nostril far from the mouth with the opening so arranged that a current of inspired air would not pass near intended food, and could not give identity of the nature of food. The Black Pointed Teguexin (*Tupinambis nigropunctatus*, fig. 9), on the other hand, has a forwardly placed opening to its nose, and the inspired air would therefore pass over intended food. I do not know the reason for these differences.

Microsmatic Mammals

When mammals are studied it is found that the microsmatic have not so close a relation between nose and mouth as have the macrosmatic species. Thus the Platypus (*Ornithorhyncus anatinus*, fig. 12) has a long bill, but unlike the Apteryx, has the nostril placed dorsally and at some distance from the tip. The animal is of aquatic habits, and as in most mammals living in the same medium, it is not guided to its food by its nose, but by its eyes (4). Although examples were given of certain macrosmatic fish, yet it is the general rule to find the opposite condition in aquatic animals because of the unsuitable nature of water for carrying scent to any distance rapidly. Furthermore, scent diffuses equally through water except when currents are present, and in consequence no marked sense of direction is given, as in the case of conditions on the earth.

Seals (*Crystophora cristata*, fig. 13) and Walruses (*Odobaenus rosmarus*, fig. 14) are both microsmatic, although both have anteriorly placed and forwardly diverted nostrils; in both however the relation is less close than in the case of the macrosmatic species. In them the nose is used for the purpose of warming inspired air, and no particular advantage would be gained by moving the anterior nostril from the position it occupies, namely, one similar to that of most terrestrial mammals.

In the Whales, Dolphins and Porpoises (*Phocaena phocaena*, fig. 15), however, the microsmatic condition (5) has allowed the nasal passage to be utilised entirely for respiratory reasons. The two anterior orifices have fused into one

blow hole, which is placed on the top of the head in such a position that it is the first part to reach the air when the animal comes to the surface. This position would make it quite impossible for a sampling of food to be carried out by the olfactory sense, even if the latter were sufficiently acute.

Macrosmatic Mammals

Of macrosmatic mammals interesting examples are found in the ant-eating Echidna (*Tachyglossus aculeatus*, fig. 16) and Great Ant Eater (*Myrmecophaga jubata*, fig. 17), both of which have a very long snout capable of entering into a nest, and a very long nasal tube with an aperture placed just over the mouth on the dorsal surface. Both are supposed to be possessed of an acute sense of smell (3), and they are indeed in need of it, because of the long distance between the mouth and eyes, and also because of the minute nature of the food. The Tapir (*Tapirus americanus*, fig. 18) has a miniature proboscis; it has a keen sense of smell (3) and no doubt uses it as a warning against attack. At the same time the downwardly diverted opening of the nares on the under surface of the projecting nose, causes the stream of inspired air to pass over all intended food and to enable discrimination to be made between suitable and unsuitable substances, irrespective of the warning of the eyes. In another place the writer has followed others in pointing out that a current of air is maintained through the nose even when the mouth is open for this especial purpose of sampling the odour of food amongst other reasons, and has attempted to show that the epiglottis has been evolved to shut off the mouth and to ensure the passage of air through the nasal instead of through the wider oral passage (6).

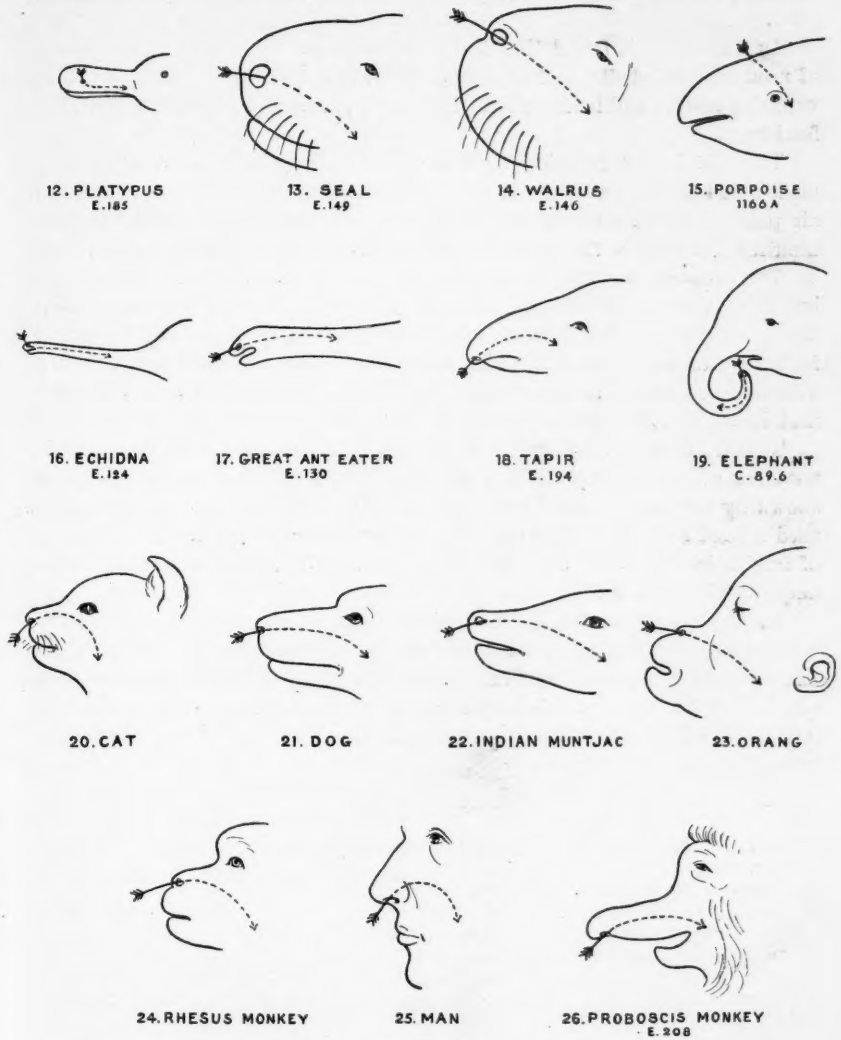
The Elephant (*Elephas africanus*, fig. 19) can find a bun with its trunk even when it cannot see it, and smells all food before putting it into its mouth; the sampling proceeds automatically during feeding, again because of the efficient epiglottis. Members of the Cat (*Felis domestica*, fig. 20), Dog (*Canis familiaris*, fig. 21) and Deer tribe (*Cervulus muntjac*, fig. 22) are all macrosmatic and in all of them the anterior nostril is in close proximity to the mouth. The sense of smell gives warning of danger as well, but if that were the only desideratum the opening of the nose could be in any forwardly directed position on the head, and would be under no necessity of lying near the mouth.

Primates

When the Primates are examined, it is found that in them the nose is used to test food, even though none of the species are markedly macrosmatic. With this object in view the nostril follows the lead of the mouth, but has not so close a relation as in some previously described species, because of the enhanced reliance which is placed on vision.

In the Orang (*Simia satyrus*, fig. 23) the muzzle is prominent but the nose is short; consequently the nostril lies slightly behind the mouth and the current of air does not pass directly over the food which is about to be taken

in. As the animal can see what it is eating, this does not inconvenience it, and is in fact entirely dependent on the supersession of smell by sight. The



Rhesus monkey (*Macacus rhesus*, fig. 24) shows a rather closer relation and has a less prominent muzzle.

In Man (*Homo*, fig. 25) the jaws have receded, and are small, but the nose has remained large in order to provide sufficient surface for the warming of

air; consequently the nose projects beyond the mouth. Although the sense of smell for distant objects is very feeble in comparison to that of Deer for instance, nevertheless, the perception of odours from near by substances is good.

As a result it is found that the olfactory organ is used to give warning of noxious food stuffs, and at times carries out its duty so efficiently that vomiting results and leads to the elimination of harmful substances from the food tract.

To assist in this function the nose is found to have its anterior opening placed on the under surface, in such a direction that the current of inspired air passes directly over every morsel as it approaches the mouth. As the mouth is invisible to the individual this arrangement is of great service.

The Proboscis monkey (*Nasalis larvatus*, fig. 26) has gone one stage further, but shows the same disposition and direction of opening of the nostril. According to E. Wiedersheim the nose of this species is small in foetal life and has forwardly directed nostrils, which undergo a change of inclination during growth of the organ, and more especially in the adult male, for it is in those individuals that the greatest length is attained (7).

That the downward direction of the nostril in man is not designed to favour warming of air, by preventing a direct current from entering the fossae, is shown by the case of Seals and Walruses. In them the organ is apparently used almost entirely for the warming of the inspired current, but no change of inclination has been brought about varying from that pertaining in the majority of mammals.

As to the true reason for the various alterations in position and for the varying degrees of propinquity of anterior nostril and mouth, enough should have been said to demonstrate that it is not for the better perception of distant scents, but for the appreciation of odours of food stuffs and the testing of intended food, and for this purpose particular modifications have been brought into existence.

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Note. The diagrams to which catalogue numbers are appended have been copied by permission from specimens in the Royal College of Surgeons Museum. The remainder are from the author's collection of specimens kindly provided by the Zoological Society of London.

A CASE OF CONGENITAL CYSTIC KIDNEY, ASSOCIATED WITH SEVERAL OTHER ABNORMALITIES

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The specimen to be described was that of a seven-months' foetus born in the Rotunda Hospital and kindly sent to the Department of Anatomy in Trinity College, Dublin.

The history of the mother received from the Hospital was as follows: K. E. aet. 19, unmarried, 1-para admitted to hospital 9. xi. 24. No abnormalities were found on general examination. Seven hours in labour. Patient was admitted with foot prolapsed through vulva and said it had been down 10 hours. Second foot brought down; patient not getting much pains, but eventually buttocks were born. The child was then seen to have a very large abdomen; extracted without much difficulty. Twenty-eight weeks development, male, weight 4½ pounds, length 16 inches; lived 2 hours. Congenital cystic kidney and other abnormalities. On receipt the foetus was found to have a greatly distended abdomen and the left foot was clubbed; there did not appear to be any other external abnormality. The specimen was then injected with 10 per cent. formalin through the umbilical vein.

On opening the abdomen the right hypochondrium and parts of the epigastrium and right lumbar region were found to be occupied by a large cystic right kidney; the liver had been much compressed and was displaced to the left. The lower parts of both lumbar regions, the iliac fossae and the upper portion of the pelvis were filled by what was at first thought to be distended large intestine, but was found on further examination to be the greatly dilated ureters, the caecum lying up under the liver in the median plane with the rest of the intestine coiled in the epigastrium and umbilical regions between the liver and the large right kidney and the ureters. Occupying the pelvic cavity and extending upwards as far as the umbilicus and backwards to the sacrum was a tense fluctuating tumour, which towards the umbilicus was quite firm and hard to the touch; this proved to be composed entirely of a distended and hypertrophied bladder, the hard and firm upper portion being due to the great hypertrophy of the bladder wall in this situation (fig. 1).

The testes were hidden from view by the dilated ureters and occupied the iliac fossae. The gubernacula could be easily recognised passing out along the inguinal canal; running across the surface of the distended ureter and bladder were the umbilical arteries and the vasa deferentia. The left kidney could not be seen nor was it palpable. There was a Meckel's diverticulum 23·5 cm. from

the ileo-caecal junction. On removing the liver it was found to be very distorted and was much more lobulated than usual; there were no cysts found in it. The foramen ovale of the heart was larger than one would expect to find in a foetus of this age.

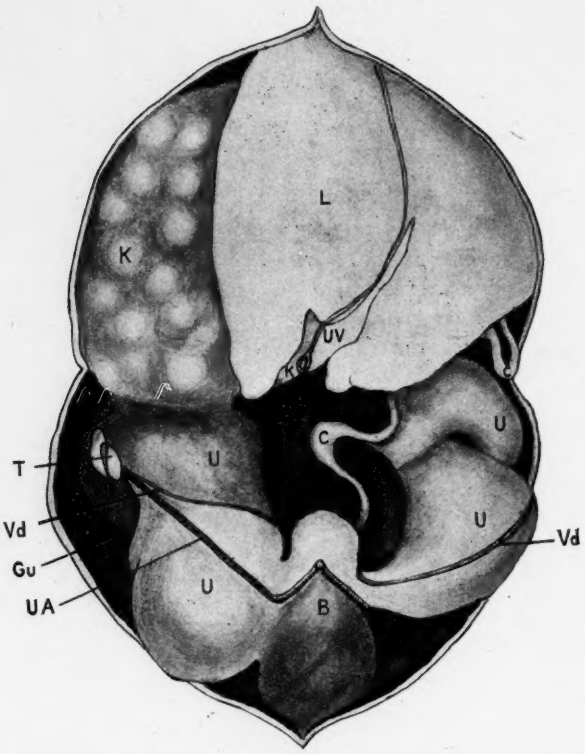

Fig. 1. Semi-diagrammatic drawing of the abdomen, after opening and removal of most of the intestine. *B.* Bladder; *C.* Colon; *Gu.* Gubernaculum; *K.* Kidney; *L.* Liver; *T.* Testis; *U.* Ureter; *U.A.* Umbilical artery; *U.V.* Umbilical vein; *Vd.* Vas deferens.

THE URINO-GENITAL SYSTEM

Kidneys. The right kidney was greatly enlarged, measuring 9·5 × 6·8 cm., its surface being studded with innumerable cysts of varying size; spread out over the supero-medial surface of the kidney was the suprarenal gland, with the inferior vena cava flattened out along its medial side (fig. 2).

On compressing the surface of the kidney, certain of the cysts could be made to collapse with an accompanying distention of the bladder, and conversely, pressure on the bladder caused a return of the cysts to their former

distended state, showing that evidently some communication existed between the cavities of the cysts and the urinary tract, i.e. they were not retention cysts. On mesial longitudinal section the kidney presented the cut surfaces of the cysts, which contained a clear dark straw-coloured fluid, and of which the whole substance of the kidney was composed, there being no normal kidney tissue at all. The pelvis of the kidney was not unduly dilated, that is, there was not a condition of hydronephrosis present, and the ureter opened by a small circular orifice large enough to admit a fine quill. The renal artery was smaller than one would expect to find in a foetus of this age.

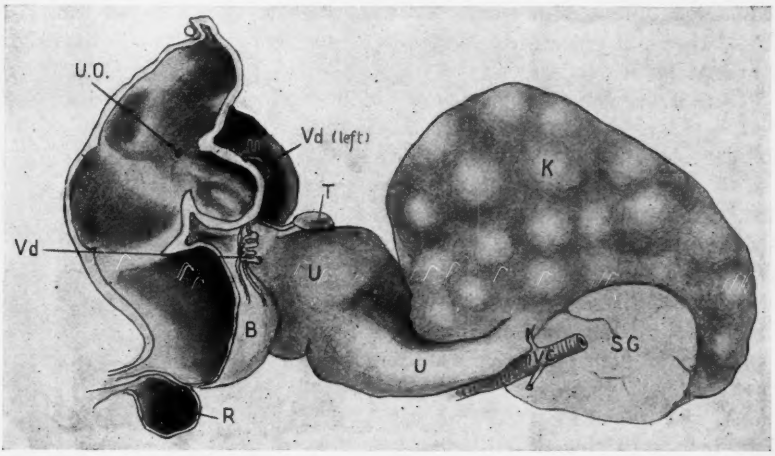

Fig. 2. Semi-diagrammatic drawing of mesial section of bladder. *B.* Posterior diverticulum of bladder; *I.V.C.* Inferior vena cava; *K.* Kidney; *R.* Rectum; *S.G.* Suprarenal gland; *T.* Testis; *U.* Ureter; *U.O.* Ureteric orifice; *Vd.* and *Vd (left).* Right and left vasa deferentia.

The left kidney was normal in position but smaller in size than usual, measuring 4·2 × 2·3 cm. It showed no signs of foetal lobulation and on close examination the surface, especially at the upper and lower poles, was seen to be covered with numerous small cysts about the size of a large pin's head. The suprarenal gland appeared normal in position and shape. The whole kidney was much firmer in consistence and altogether presented a more normal appearance than that of the opposite side, and on mesial section, it was found that the small cysts involved mainly the periphery of the organ; the pelvis was considerably dilated, so much so indeed that the kidney substance measured only 4 mm. in its thickest part; the opening of the ureter was larger than on the right side, in fact there was a condition of commencing hydronephrosis.

On microscopical examination the entire periphery of the kidney was composed of cysts of varying size, and in between them here and there were much distorted and compressed glomeruli. Nearer the centre of the kidney

were numerous glomeruli, many of them appearing larger than usual, with, frequently, distended and thickened capsules. In the medullary portion were found tubules in varying degrees of distention, some appearing normal while others were greatly dilated. It was noticeable in the case of several of the dilated tubules that the wall of the tubule was separated from the surrounding kidney tissue by a considerable space; in the cortical part of the kidney too, many of the tubules were distended. Most of the cysts in the periphery appeared to be closed spaces and to have no communication with the uriniferous tubules, but here and there a communication was found to exist between the cysts and the uriniferous and collecting tubules by means of a short and constricted tubule. Throughout the whole kidney there was an excess of fibrous tissue, of which there seemed to be a great proliferation in the neighbourhood of the pelvis.

Ureters. The condition in each of the two ureters was very similar; they were both greatly distended, sacculated and convoluted, being large enough here and there to admit two or three fingers (figs. 1, 2 and 3); the convolutions were such that it was a matter of considerable difficulty to pass a probe along the duct, the sacculation having resulted in an infolding of the wall so as almost to obstruct completely the lumen of the vessel. There was communication between the two ureters and the bladder, pressure on the right kidney causing distention of the opposite ureter. Each of the ureters opened by a small orifice into the bladder (fig. 2), the ureteric side of the opening being guarded by a sort of valve-like fold of the mucous membrane. Stretched out over the surface of the distended ureters were (*a*) the internal spermatic vessels passing to the testes, which were lodged in the iliac fossae and overlapped by the lateral edge of the ureter; (*b*) the umbilical arteries which passed in an anterior and medial direction from under cover of the testis to the bladder, along the antero-inferior surface of which they passed towards the umbilicus, where the two vessels appeared to unite; (*c*) the vas deferens which ran transversely across the posterior surface of the bladder and whose course will be discussed later.

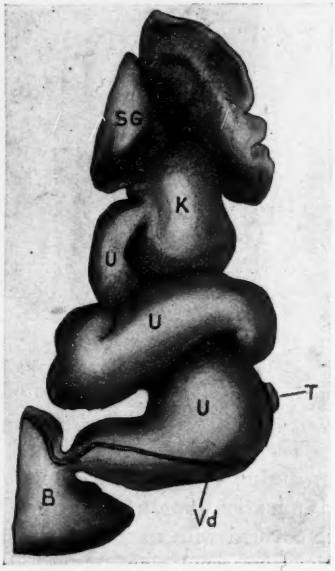

Fig. 3. Semi-diagrammatic drawing to show convolution and distention of left ureter. *B.* Bladder; *K.* Kidney; *S.* Spleen; *S.G.* Suprarenal gland; *T.* Testis; *U.* Ureter; *Vd.* Vas deferens.

Bladder. The bladder formed a tense swelling in the pelvis and extended

upwards to the umbilicus, where it formed a hard tumour-like mass; the organ was irregular in shape, presenting a sort of pouch-like diverticulum which was directed from its postero-inferior part against the sacrum; from the bottom of this pouch to the apex measured 8·6 cm. The bladder was crossed anteriorly in an upward direction by the umbilical arteries and posteriorly in a transverse direction by the vasa deferentia. The apex of the bladder extended right up to the umbilicus, there was thus no urachus. On mesial section the bladder wall was found to be greatly hypertrophied, measuring 5 mm. at its thickest part, and the cavity was marked by numerous diverticula and ridges due to hypertrophy of the underlying muscle; it presented, in short, very much

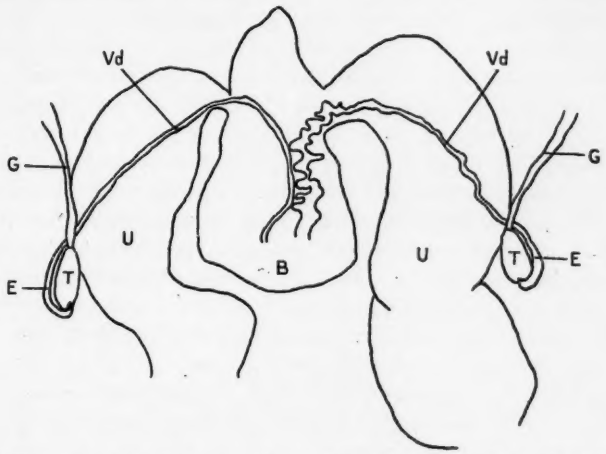

Fig. 4. Diagram representing course of vasa deferentia. *B.* Bladder; *E.* Epididymis; *G.* Gubernaculum; *T.* Testis; *U.* Ureter; *Vd.* Vas deferens.

the appearance of the bladder in a case of longstanding enlargement of the prostate (fig. 2).

One of the diverticula has already been mentioned as extending in a downward and backward direction towards the sacrum; this diverticulum occupied the lower part of the bladder, and had a somewhat different appearance from the upper part of the organ; its walls were thin, measuring only 1 mm. in thickness, and muscular fibres were but weakly developed in it, especially in its posterior wall; this part of the bladder appeared to have undergone a distention rather than a hypertrophy, and was separated from the upper part of the bladder by a definite muscular ring. In the bottom of the diverticulum was a semilunar valve-like fold of the mucous membrane opening in a downward direction, with a slight ridge marking each horn of the crescent. The openings of the ureters were by two small orifices which it was by no means easy to differentiate from some of the smaller diverticula or loculi of the bladder.

Urethra. Unfortunately I made a mesial section of the whole infant before examining the urethra. I was nevertheless able to satisfy myself that it was patent throughout its whole length—a fine glass probe, with a blunt rounded end, could be passed without difficulty along it. The prepuce was closely adherent to the glans penis and was not easily reflected from it and was somewhat twisted round the end of the penis, though not to such an extent as to cause any obstruction to the outflow of urine. The external urinary meatus was quite clear and patent.

Testes. The two testes appeared normal in size and shape and occupied the position already stated.

Vas deferens. The two vasa deferentia ran transversely medially across the posterior surface of the bladder, but the appearance of each differed considerably. The right had the more normal appearance of the two, and was quite definite, large and convoluted all the way from the testis to its termination; the left vas was very slender and it was with difficulty that it could be traced at all, and in place of being convoluted, it ran a perfectly straight course, except for a small part near its origin from the epididymis. The two ducts passed medially from the testes, being spread out over the distended ureter, on to the posterior surface of the bladder till they reached the middle line where they turned vertically downwards, the left being in close apposition to the convolutions of the right. They ran down on the posterior surface of the bladder until they reached its dilated posterior diverticulum, where they pierced the bladder wall on each side of the middle line (fig. 4), opening on the ridges which marked the horns of the semilunar fold of mucous membrane already mentioned. There was no sign of any seminal vesicles.

Prostate. It was not possible to demonstrate with certainty any prostate gland.

Beyond a club-foot on the left side and a rather large foramen ovale in the heart, the foetus did not exhibit any other abnormality.

DISCUSSION

It is worth noticing the combination of abnormalities found in this case—the condition of the urino-genital system, Meckel's diverticulum, club-foot, lobulation of the liver and the size of the foramen ovale in the heart. No cysts of the liver were found in this case, but it is not uncommon to find cysts of the liver associated with cystic disease of the kidney; Eisendrath (4) states that cysts of the liver occur in about 18 per cent. of cases. In cystic disease of the kidneys the condition may be associated with either great increase or diminution in the size of the organs; Leopold and Kunstler (7) describe a case in an infant of 3 months, in which the kidneys were much enlarged; Greene (5), on the other hand, gives an account of the condition in a girl of 3 years, in whom both kidneys were atrophic and much reduced in size. The present case shows great enlargement on the right side and diminution on the left. The condition

appears to be more usual between the ages of 40 and 50, and is more frequently bilateral than unilateral (Barnett (2)).

As regards the causation of the condition, several now well-known theories have been advanced, of which the one that has met with most general acceptance is that the condition is due to a failure of union between the two developmentally distinct parts of the kidney, that is, a failure of union between the uriniferous and collecting tubules. Kampmeier (6) has recently put forward a suggestion that there is an apparently constant appearance of renal cysts at a certain period of foetal life; he has been able to observe: (*a*) the existence of a vestigial primary generation of uriniferous tubules; (*b*) the occasional cystic transformation of such vestigial tubules; (*c*) the early communication of the next or second order of uriniferous tubules with the collecting ducts of the corresponding order; (*d*) the temporary detachment of most of these tubules from the secondary collecting ducts and their reunion with ducts of the 4th and 5th orders; (*e*) the later permanent separation of these uriniferous tubules from the ducts and the cystic transformation of them. Neither of these theories seems to be applicable to all cases, for in both one would expect the cysts to be closed cavities and not to have any communication with the pelvis of the kidney; certainly the cysts are frequently of the closed type, but in some few it can be demonstrated that there is a communication between the cavity of the cyst and that of the ureter. If the condition were due to an obstruction to the outflow of urine from the uriniferous tubule to the collecting duct, it seems that when the condition is in an early stage, one should be able to recognise a general enlargement of the uriniferous tubule and not of the collecting duct, and that it should not be possible to demonstrate small spheroidal cysts. Greene (5) was able to show, in the case already cited, by means of a wax plate reconstruction that the cysts were in no sense retention cysts, but were due to a cystic dilatation especially of the second part of the proximal convoluted tubule. It seems possible that when the condition which had commenced in this manner had developed further, the cysts so formed would cause pressure here and there on neighbouring dilated tubules and would thus obstruct the lumen of the tubule, which by an invasion of fibrous tissue, of which there is usually a large amount in these cases, would be completely obliterated and so cause the formation of the closed cyst. It has already been mentioned that in the present case a communication between certain of the cysts in the right kidney and the cavity of the bladder could be demonstrated by means of pressure, and this was confirmed by examination of the kidney when the cysts were opened, when it was found that some of the cysts were not closed cavities but had small tubules leading from them. This could also be demonstrated by microscopical examination of the left kidney, which was affected to a much less degree than the right, and in which certain of the large peripheral cysts were found to have a small tubule leading from them which, in serial section, could be traced to a collecting duct. There was a large amount of fibrous tissue in this specimen, and it seems possible

that the shutting off of the closed cysts may be due to an invasion of fibrous tissue and indeed that it may have been the original cause of the primary dilatation of the tubules.

The condition of the bladder in the present case is most unusual, and it raises the interesting question as to when the foetus commences to excrete urine. That there must have been a very considerable secretion of urine is evidenced by the state of dilatation of the whole urinary tract, which leads one to wonder how so much urine can have been secreted by two such indifferently functioning kidneys.

One would expect to find some obstruction in the urethra in such a case as this, but there does not appear to have been any obstruction along the length of the urinary tract; similar cases of hypertrophy of the bladder without urethral obstruction have been described on previous occasions, though they do not appear to be frequent (Ballantyne (1)). As a cause of the hypertrophy of the bladder, Thomson (8) suggests that the condition is comparable to that of congenital hypertrophic stenosis of the pylorus, and may be due to a lack of co-ordination in the bladder musculature; that when the bladder as a whole contracts, there is a simultaneous contraction of the sphincter vesicae, ultimately resulting in a hypertrophy of both sets of muscles.

A distention of the ureters and hydronephrosis may exist without any hypertrophy of the bladder and without any urethral obstruction (Blackwood (3)).

As regards the large diverticulum of the bladder in the present case, and the relation to it of the vasa deferentia, it is probable that this part of the bladder represents that part of the uro-genital sinus which normally forms the prostatic portion of the urethra, and which in this case has become incorporated in the bladder together with the seminal vesicles.

SUMMARY

The case shows multiple abnormalities—cystic kidneys, unilateral hydronephrosis, dilatation of the ureters to an enormous extent, hypertrophy and dilatation of the bladder, abnormal arrangement of seminal ducts, apparent fusion of the two umbilical arteries at the umbilicus, a Meckel's diverticulum, a much lobulated liver, a large foramen ovale and a club-foot.

The cysts of the kidneys are of various sizes, some appear to be retention cysts while others communicate with the rest of the urinary tract. It is suggested that the closed cysts may have become shut off by means partly of the pressure of neighbouring cysts and partly by a marked proliferation and subsequent invasion of fibrous tissue.

The bladder is much hypertrophied and dilated and presents in its postero-inferior part a large diverticulum, into which open the vasa deferentia; it is suggested that this part of the bladder represents that part of the uro-genital sinus which normally takes part in the formation of the prostatic portion of the urethra.

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AN INVESTIGATION OF THE OCCURRENCE, DISTRIBUTION AND HISTOLOGICAL STRUCTURE OF THE EMBRYONIC REMAINS IN THE HUMAN BROAD LIGAMENT[1]

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INTRODUCTION

Cystic structures in the broad ligament are not uncommonly found both at operation and in the post-mortem room—some of them attaining to an enormous size. Their origin is attributed to the embryonic remains found in the broad ligament and although a number of theories have existed with regard to the exact origin of these cysts, the problem is still unsolved. Bantock (1873)(2) claimed that all cysts of the broad ligament, whether above or below the Fallopian tube, were parovarian in origin, whereas Kossmann (1903)(15), working on the histology of the cyst wall, suggested that all were Müllerian, i.e. had developed from accessory fimbriae or the Fallopian tube. Alban Doran in 1884(8), realised that many were not parovarian in origin, but he was not able to give a precise origin, until, in a paper written in conjunction with Keith in 1910(13), he assigned the origin of all large cysts of the broad ligament to the rete or junctional tubules of Allen(1), in contradistinction to the smaller cysts which were of Wolffian origin. Sampson Handley(10) had previously (1903) shown that cysts situated above the Fallopian tube, were developed from accessory fimbriae and were, therefore, Müllerian, and he took as proofs of this, the fact that the walls of the cysts showed plications, and the existence of a communication between the cavity of the cyst and the main Fallopian tube. Thus it seems important and necessary, as suggested by Keith(13), that a complete investigation of the embryonic remains, independently of cysts and anomalies, should be undertaken, especially as, with the

[1] Being an extract from a thesis accepted for the Degree of Doctor of Medicine of the Victoria University of Manchester, and awarded commendation, May 1923.

exception of the workers quoted, the subject has gained little attention. With these facts in view it was decided to examine histologically a series of human broad ligaments, to discover in what proportion of cases these embryonic remains persist into adult life, and what proportion tend to increase or diminish in size in later years, and to determine, if possible, their fate. That growth does take place, in certain cases, can be demonstrated in such a series of dissected specimens as may be seen in the Museum of the Royal College of Surgeons, London, but whether this is constantly the case, is not stated. Professor Keith (13) found that the Wolffian body could be very clearly defined in the new-born subject, though this body, in his and Percival Cole's opinion (6), reaches its higher development quite late in adult sexual life—about the 35th to the 45th year—in later years tending to become obliterated by conversion of the tubules into solid cords of fibrous tissue (Cole (6)). On the other hand, Rielander (1904) (18) found that the remains of the paroophoron could only be detected with certainty up to the 5th year.

The investigations have been carried out mainly by histological methods—the broad ligament of one side having been used for serial sections. In a number of cases, gross dissection has been used to demonstrate the anatomy of the tubules on the remaining side. By these means it has been possible to map out in diagrammatic form, with fair accuracy, the distribution of the embryonic remains throughout the mesosalpinx and mesovarium.

It was hoped that it might prove instructive to compare the histological structure of the wall of the embryonic tubules with that of certain cysts found in the broad ligament, and this was done in a number of cases. The chapter referring to this part of the original work has been reserved for publication at a later date.

The term "embryonic remains" is used to include:

1. The Wolffian body, or organ of Rosenmüller, consisting of a duct running parallel to the Fallopian tube, with a number of small blind tubules opening at right angles into it.

2. The paroophoron situated in the mesosalpinx but nearer to the uterus than the former.

3. Gärtner's duct running parallel to the body of the uterus and inferior to the round ligament of the ovary.

4. The junctional cords or tubules corresponding with the rete testis in the male, and found in the mesovarium or hilum of the ovary.

No attempt has been made to investigate the embryology of the broad ligament.

In writing up the work, it has been found convenient to divide it up into various sections, commencing with the gross anatomy, and each section has been arranged in the order of age of the cases investigated.

ACKNOWLEDGMENTS, SOURCE OF MATERIAL, ETC.

My best thanks are due to Professor J. S. B. Stopford, at whose suggestion this work was undertaken two years ago, for his ever ready help and interest, and I am glad of this opportunity to express my gratitude. He has placed at my disposal dissected specimens from the anatomical museum, as well as apparatus and materials from the histological department, and full use has been made of this privilege.

I am also indebted to Mrs Sellars, B.Sc., for the time and trouble she has devoted to helping me with the histological technique, and for the interest she has shown in the progress of the work. Many of her suggestions have been of the utmost value.

By kind permission of Professor Dean and Professor Shaw Dunn, a number of specimens have been obtained from the post-mortem room of the Manchester Royal Infirmary, and I wish to record my thanks for this courtesy. Specimens from autopsies upon infants have been obtained from the Manchester Babies' Hospital.

I wish to acknowledge the assistance received from Miss E. Wade, M.B., Ch.B., during the last three months in the cutting and staining of serial sections. Up to this time, I had prepared, cut and stained all the tissues myself.

I am indebted to Miss Howe for the dissection of specimens to demonstrate gross anatomy.

The photographs have been done by Mr H. Gooding of the Anatomy Department, from my own sketches.

PART I. TECHNIQUE

A. Histological

Nearly all the specimens have been obtained within 24 hours of death, and have been fixed in a 10 per cent. solution of commercial formaldehyde. Where possible, the uterus with broad ligament was dissected out intact, and was first carefully examined with the naked eye and dissecting microscope. In some cases, the Wolffian body could be recognised without dissection. Small cysts or hydatid appendages were seen, and in every case a careful note was made for comparison with the microscopic appearances. Before fixation, the uterus with broad ligament was pinned out, with the posterior surface uppermost, upon a paraffin wax block, tension on any one part being avoided. Certain landmarks, e.g. the Fallopian tube, ovary and round ligament of the ovary, were thus easily visible, and definite blocks of tissue could be cut and embedded in as uniform a manner as possible.

Four blocks of tissue were cut from one side of each specimen (fig. 1, right side):

(*a*) A triangular piece of tissue, bounded by the Fallopian tube, the round ligament of the ovary, and a line drawn at right angles to the tube from the caudal pole of the ovary.

(*b*) A rectangular piece of tissue, cut parallel to the ovary, including the Fallopian tube and half the mesosalpinx, as far as the cranial pole of the ovary.

(*c*) A rectangular piece of tissue, including the mesosalpinx left from block (*b*), the mesovarium and a small portion of the ovary.

(*d*) A rectangular block cut from the round ligament of the ovary above to the level of the cervix of the uterus below, bounded internally by the uterine wall and extending half an inch externally into the broad ligament.

After seven specimens had been examined, the method of cutting the blocks was altered, as, by a new suggestion, more accurate localisation was anticipated, and the piece of mesosalpinx, lying lateral to the ovary, was thus included, this having previously been rejected.

It had also been found impossible, after examining the first seven series of sections under the microscope, to differentiate between the tubules of the

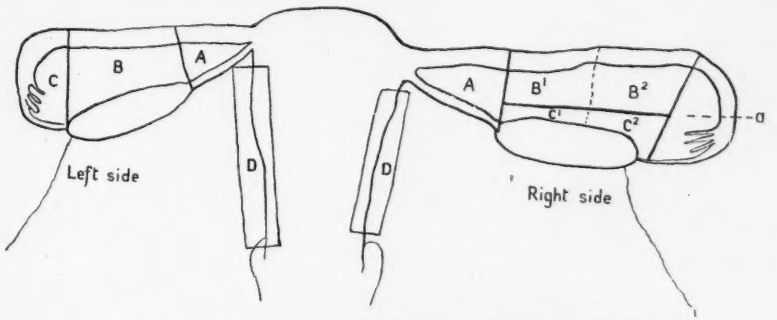

Fig. 1. Diagram of posterior surface of uterus and broad ligament:
Right side indicates method of cutting first 7 specimens.
Left side indicates method of cutting all other specimens.
(*a*) Rejected.

Wolffian body and the junctional cords found in the mesovarium, merely by such a comparatively rough method as cutting the blocks as explained above, so it was decided to combine the tissue included under (*b*) and (*c*) in one block named (*b*). Thus all the later specimens were cut in the following manner (fig. 1, left side);

(*a*) See p. 412.

(*b*) An oblong piece of tissue, bounded above by the Fallopian tube, below by the ovary and including the mesovarium, internally by the line drawn from the caudal pole of the ovary at right angles to the Fallopian tube, and externally by a similar line drawn parallel from the cranial pole of the ovary.

(*c*) The rest of the mesosalpinx, including the fimbriated end of the tube and the ovarian fimbria.

(*d*) See p. 413.

The tissues were then dehydrated by means of increasing strengths of alcohol, and cleared in xylol, preparatory to being embedded in paraffin with

melting point 54° C. Serial sections of a thickness of 20μ were then cut—every 50th section being mounted for examination, while the intermediate sections were reserved for future examination if required. In most cases the whole block was cut, but in the case of certain blocks (*d*) a series of 200 to 300 sections was cut and a piece of the block 1 cm. in thickness was kept, after which another series of sections was cut.

As a routine practice, all mounted serial sections were stained with haemalum and eosin.

Where tubules were found by microscopic examination to be present, a further number were mounted, and stained by various methods with a view to demonstrating their histological structure. The stains used were:

Methylene blue and alcoholic eosin. Mallory's stain. Van Giesen.

B. Anatomical

The method of dissection used was to strip off the peritoneum forming the posterior surface of the mesosalpinx, cutting away portions of the ovary where necessary to expose the tubules clearly. In this way, the tubules of the Wolffian body were left lying upon the anterior peritoneal layer of the mesosalpinx.

PART II. GROSS ANATOMY

In every case (fifteen in all—of which dissections were made on both sides in two specimens, and on one side in the remaining thirteen), it was possible to demonstrate, by gross dissection, the presence of the Wolffian body, including vertical tubules and horizontal duct. The following table (Table I) explains the distribution and number of the tubules, and figs. 2 to 6 are actual photographs of specimens dissected.

Table I. *Dissected specimens—to illustrate distribution of Wolffian Body (fig. 1, left side).*

No. of Case		Age	Wolffian body visible before dissection	Position of tubules	No. of vertical tubules	Diameter of horizontal duct compared with that of tubules
II	R.	8½ months foetal	No	Block (*b*)	8	Greater
II	L.	8½ months foetal	No	Blocks (*b*) and (*c*)	8	Greater
X	L.	9 months foetal	Yes	Block (*c*)	Not countable	Greater
XII	R.	9 months foetal	No	Blocks (*b*) and (*c*)	4	Not greater
XII	L.	9 months foetal	No	Block (*c*)	5	Not greater
XIV	L.	8 weeks	No	Block (*c*)	2	Not greater
XVI	R.	6 months	No	Block (*c*)	5	Greater
IX	L.	7 months	No	Blocks (*b*) and (*c*)	8	Greater
XVIII	R.	7 months	No	Blocks (*b*) and (*c*)	9	Greater
XV	R.	3 years	No	Block (*c*)	9	Greater
XVII	R.	3 years	No	Blocks (*b*) and (*c*)	8	Greater
XIX	L.	13 years	No	Blocks (*b*) and (*c*)	9	Not greater
XX	R.	23 years	No	Blocks (*b*) and (*c*)	9	Not greater
XXII	L.	43 years	No	Block (*c*)	6	Greater
XI	L.	50 years	Yes	Blocks (*b*) and (*c*)	8	Greater
XIII	L.	50 years	No	Blocks (*b*) and (*c*)	10	Greater
XXI	L.	51 years	No	Blocks (*b*) and (*c*)	10	Greater

Fig. 2. Dissection of Case XVI—age 6 months—showing posterior aspect of right broad ligament. (*a*) Wolffian body, consisting of horizontal duct and vertical tubules, lying lateral to the ovary and crossed by a blood vessel. (*b*) Ovary. (*c*) Uterus.

Fig. 3. Dissection of Case XIX—age 13 years—posterior aspect showing left broad ligament and ovary.
(*a*) Wolffian body of large size. (*b*) Small cyst. (*c*) Uterus (cut). (*d*) Ovary.

Fig. 4. Dissection of Case XXII—age 43 years.
(*a*) Cyst arising in wall of Fallopian tube. (*b*) Wolffian body. (*c*) Cyst of unknown origin, but not connected with Wolffian body. (*d*) Cut surface of uterus.

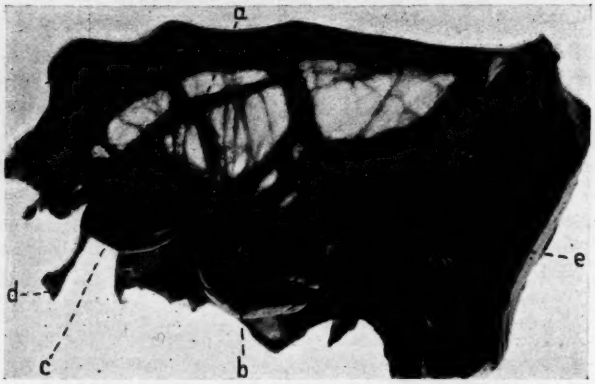

Fig. 5. Photograph of Case XV—age 50 years—taken by transmitted light and showing posterior aspect of left broad ligament.
(*a*) Wolffian body, with horizontal duct. (*b*) Ovary (cut open). (*c*) Cyst (collapsed). (*d*) Accessory fimbria. (*e*) Cut surface of uterus.

Fig. 6. Dissection of the same specimen (Case XV).
(*a*) Wolffian body. (*b*) Ovary (cut open). (*c*) Accessory fimbria.

PART III. MICROSCOPICAL ANATOMY

The aim of the microscopical examination of one side of twenty broad ligaments has been:

(*a*) To differentiate the microscopical appearance of the embryonic remains, which are known to have a varied embryological origin.

(*b*) To demonstrate age changes in the histology of the tubules (see Part IV).

(*c*) To map out accurately the distribution of the various types of tubules by means of diagrams.

(*d*) To enumerate the tubules found in each specimen, so that a comparison could be made of the actual number of tubules at different ages. This proved to be impossible of accomplishment, as each tubule was probably cut through several times in the same section.

A large portion of the original thesis was devoted to an accurate description of the individual sections examined, there being as many as 70 sections from one case (i.e. mounting one section out of every 50 cut). But as it is not possible to publish this part of the work in its entirety, an attempt has been made to summarise the details in the table appended (Table II). Where mention is not made of the number of sections examined, it is understood, either that the whole block was not cut, or that instead of mounting every 50th section cut, a large number of sections was mounted, representative slides being chosen for staining and examination (see Part I). This latter method was only used in Cases I and III and in the case of certain blocks (*d*). Figs. 7 to 13 illustrate the anatomical position and distribution of the tubules in certain cases chosen as being illustrative of the various ages.

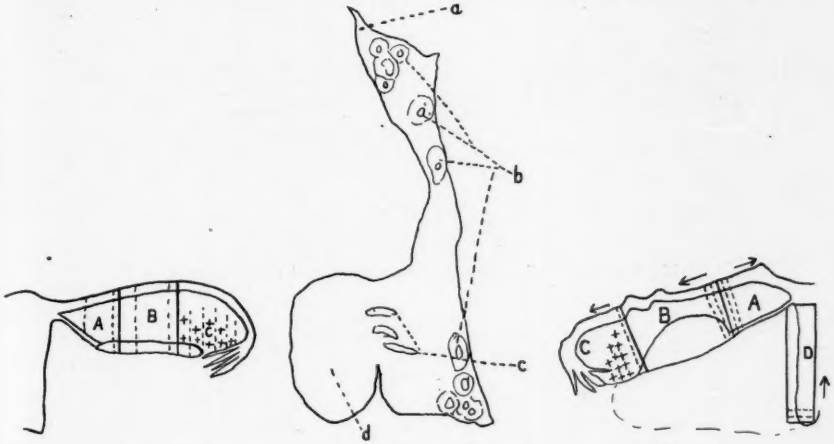

Fig. 7 Fig. 8 Fig. 9

Fig. 7. Case I—right side, posterior aspect—age 8 months foetal.
Fig. 8. Case I—diagram of section of block (*c*).
(*a*) Cut edge of mesosalpinx. (*b*) Tubules of Wolffian body. (*c*) Blood vessels. (*d*) Ovary.
Fig. 9. Case XV—left side, posterior aspect—age 3 years.
– – – – indicates plane of cutting of sections. + + + + indicates position of tubules.

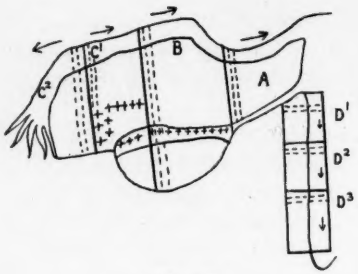

Fig. 10

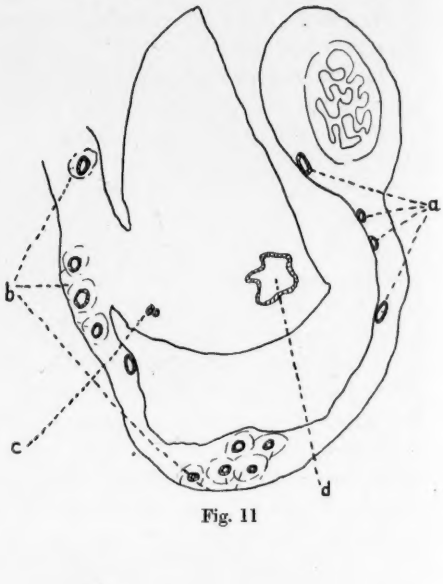

Fig. 11

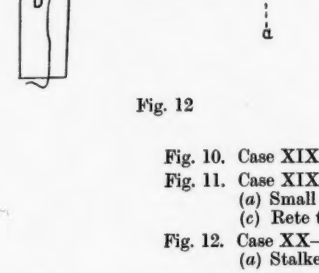

Fig. 12

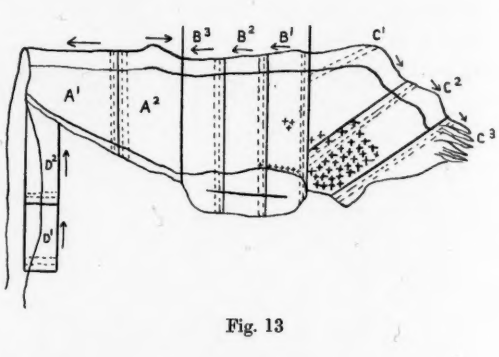

Fig. 13

Fig. 10. Case XIX—right side, posterior aspect—age 13 years.
Fig. 11. Case XIX—diagram of section of block (*b*).
(*a*) Small cysts, showing epithelial lining. (*b*) Wolffian tubules.
(*c*) Rete tubules. (*d*) Graafian follicle cyst.
Fig. 12. Case XX—left side, posterior aspect—age 23 years.
(*a*) Stalked cyst seen with naked eye.
Fig. 13. Case XI—right side, posterior aspect—age 50 years.
– – – and arrows indicate planes of cutting. + + + indicate position of tubules.

Table II. *Microscopical Anatomy of* 20 *broad ligaments.*

Case		Age	Cause of Death	Wolffian body visible with naked eye	Block (*a*)			Block (*b*)					Block (*c*)					Block (*d*)	
					Number of Tubules found			Number of Wolffian Tubules					Number of Wolffian tubules found						
					Number of Sections Examined	Minimum	Maximum	Number of Sections Examined	Minimum	Maximum	Wolffian Duct found	Presence of Rete Tubules	Number of Sections Examined	Minimum	Maximum	Wolffian Duct found	Presence of Rete Tubules	Number of Sections Examined	Gärtner's Duct found
I	R.	8 months foetal	Not known	No	—	0	0	—	0	0	0	0	—	0	16	+	+	Not examined	
X	R.	9 months foetal	Not known	Yes	5	0	0	10	0	7	0	0	11	0	14	0	0	12	0
XIV	R.	8 weeks	Congenital jaundice	No	8	0	0	10	0	7	0	+	9	0	7	0	0	8	0
VII	R.	4½ months	Chronic dyspepsia	No	8	0	0	7	0	0	0	0	11	Part of Block rejected			0	11	0
VII	L.	4½ months	Ditto	No	Not examined			23	0	13	0	0	Included in Block (*b*)					Not examined	
XVI	L.	6 months	Congenital syphilis	No	10	0	0	12	0	1	0	+	10	0	19	?	0	11	0
IX	R.	7 months	Chronic dyspepsia	No	6	0	0	8	0	3	+	0	11	0	6	0	+	10	0
XVIII	L.	7 months	Broncho-pneumonia	Yes	8	0	0	14	0	21	0	+	10	0	11	0	0	21	0
XVII	L.	3 years	Meningitis (6 hours history)	No	13	0	0	19	0	0	0	0	12	0	21	0	0	21	0
XV	L.	3 years	Empyema and pericarditis	Yes	15	0	0	13	0	0	0	0	10	0	9	0	0	16	0
XIX	R.	13 years	Tuberculous meningitis	Yes	16	0	0	19	0	12	0	+	14	0	28	0	0	20	0
V	L.	15 years	Ditto	No	18	0	0	26	0	15	0	0	10	0	0	0	+	Not examined	
XX	L.	23 years	Diabetes	Yes	14	0	0	23	0	0	0	+	12	0	10	0	+	—	0
III	R.	24 years	Cerebral tumour	No	—	0	0	—	0	0	0	0	—	1	2	+	0	—	0
IV	R.	29 years	Septicaemia	No	11	0	0	9	0	8	0	0	9	2	4	0	0	9	0
VIII	L.	36 years	Tuberculous bronchiectasis	?	16	0	0	18	0	0	0	0	16	0	7	0	0	9	+
XXII	R.	43 years	Operation specimen	No	30	0	0	26	0	0	0	+	19	0	12	0	0	—	0
XI	R.	50 years	Cerebral haemorrhage	No	18	0	0	17	0	11	0	+	25	0	34	0	0	—	0
XIII	R.	50 years	Peritonitis	No	12	0	0	21	0	3	0	+	8	0	3	0	+	—	0
XXI	R.	51 years	Not known	No	17	0	0	28	0	9	0	+	10	0	11	0	0	—	0
VI	L.	65 years	Cirrhosis of liver	No	15	0	0	27	0	0	0	+	26	0	24	0	0	—	+

PART IV. HISTOLOGY

Case I, age 8 *months* (*foetal*).

Each Wolffian tubule is cylindrical and lined by a single layer of cubical epithelium placed upon a basement membrane. The nuclei are large, and deeply stained and there is a small amount of eosinophil granular protoplasm. There is no submucous layer. The muscular coat is chiefly longitudinal in arrangement, these longitudinal unstriped fibres forming the internal muscular coat. There is an outer fibrous coat of fairly dense connective tissue containing a number of small blood vessels. This description suffices for the majority of the tubules, but some of them show a few scattered smooth muscle cells external to the longitudinal ones (fig. 14). The tube with the large lumen—

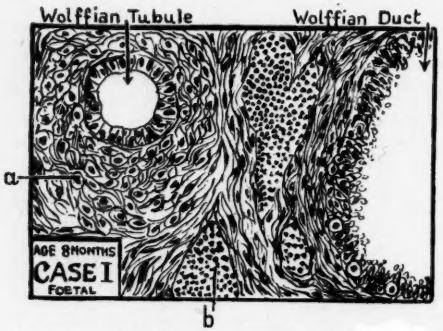

Fig. 14. Microscopical drawing of Wolffian tubule and duct.
(*a*) Smooth muscle fibres cut transversely. (*b*) Blood vessel.

the Wolffian duct—shows an epithelial lining composed of a layer of tall columnar epithelial cells, placed upon an incomplete basement membrane. The number of layers appears to vary in different parts of the same section, and also in different sections, from one to three. Of course, this may be due to oblique cutting. Amongst the cells of the basal layer are a number of large oval cells containing a large nucleus with an abundance of clear protoplasm. The muscular coat consists of smooth muscle fibres arranged in a circular manner, and there is a fibrous coat externally, containing a few small blood vessels.

The junctional tubules or rete spaces are flattened, irregular spaces, lined by low cuboidal epithelial cells with large nuclei. These are surrounded by a mass of loose fibrous connective tissue, in which no smooth muscle fibres are seen, with a rich blood supply, carried in minute blood vessels, not capillaries. No definite wall outside the epithelium can be said to exist.

Case X, age 9 *months* (*foetal*).

The epithelial lining of each Wolffian tubule consists of a single layer of columnar cells placed upon a basement membrane. The nuclei are large,

arranged side by side at the base of the cell, and stain a pale blue colour with methylene blue. A few of them show a reticular formation and a nucleolus. The cytoplasm is finely granular and eosinophil, the cells lining some of the tubules being clearer than others. The wall of the tube is thicker than that of the small arteries lying in the vicinity and consists for the most part of longitudinally arranged smooth muscle cells, although some circular muscle fibres can be detected. Interlacing between the muscle cells, white connective tissue fibres can be seen. Outside, is a fibrous coat of loose connective tissue, which is clearly differentiated in sections stained by Mallory's method.

Case XIV, age 8 weeks.

The Wolffian tubules in (*b*) and (*c*) show a well marked epithelial lining of cubical type, external to which is a muscular coat. The inner region of this is composed of longitudinal smooth muscle cells, and the outer, of circularly arranged cells. There is an ill-defined fibrous connective tissue coat. The rete spaces (fig. 15), on the other hand, are irregular in shape, and are lined by columnar epithelium of a less regular type, placed upon a basement membrane.

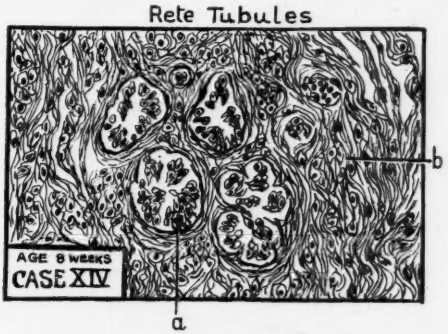

Fig. 15. Microscopical drawing of rete tubules.
(*a*) Epithelial lining. (*b*) Connective tissue.

The cytoplasm is clear. They appear to possess no wall, in many cases, but in one section four spaces lying close together show a loosely arranged fibrous coat, containing a very few scattered smooth muscle fibres (fig. 15). There are several small blood vessels in relation with them. Towards the end of the series the wall is quite absent, the epithelium being embedded in a mass of closely packed fibrous tissue in the hilum of the ovary.

Case VII, age 4½ months.

The epithelial lining of the tubules is cubical in type and resting on a basement membrane. Outside this there is a longitudinal smooth muscle coat with some circular fibres lying externally. There is an outer fibrous tissue coat containing blood vessels. The longitudinal arrangement of the muscular coat is well shown in sections taken longitudinally through the tubules.

Case XVI, age 6 months.

The Wolffian tubules in block (*c*) are lined by an epithelium which varies from a cubical to a columnar shape, the nuclei of which stain very deeply, the base of the cells resting on a basement membrane. There is an inner longitudinal and outer circular smooth muscle coat, and in many of the tubes only a scanty vascular connective tissue sheath. Where the tubules are dilated and contain coagulated material, the wall is thinned at the expense of the circular rather than the longitudinal coat, which shows well. The epithelium retains its columnar character. The tubule, suggested as the duct, shows a very well developed longitudinal coat, but only a few scattered circular muscle cells.

The rete spaces seen in block (*b*) are lying close to a blood vessel, the muscular coat of which appears to send cells to surround them. The epithelial cells are of a cubical type and both nucleus and cytoplasm stain deeply, the spaces being irregular in shape. The basement membrane is not well marked. These epithelial spaces are surrounded by loose connective tissue, but as stated above, muscle cells derived from neighbouring blood vessels are lying close to them. Others are more regular in shape, and the epithelial cells are more regularly disposed, but surrounding them are a few scattered connective tissue fibres and nuclei.

Case IX, age 7 months.

Upon examining a large tubule seen in block (*b*) under the oil immersion lens, the epithelium is seen to be cubical in type and placed upon a very well defined basement membrane. The nuclei are large and nearly fill the cells, the protoplasm of which is granular and deeply stained, apparently of neutrophil reaction. The wall of the tube consists of two layers of smooth muscle fibres—the inner being arranged longitudinally and the outer circularly. Externally, there is a fibrous coat of loose connective tissue containing several blood capillaries. There is no submucous layer. The longitudinal muscular coat of the other tubules is not so well defined, though their histological appearance is very similar.

The rete or junctional tubules are again spaces in the surrounding mesovarial connective tissue, and lined by cubical epithelium. They are devoid of muscular or fibrous coats.

Case XVIII, age 7 months.

The Wolffian tubules in blocks (*b*) and (*c*) are lined by a columnar epithelial lining placed upon a basement membrane, the cells having a clear cytoplasm which stains palely. Outside this is a longitudinal muscle coat consisting of several layers of smooth muscle cells, and outside this again is a circular muscle coat, which is thinner than the longitudinal coat. There is an outer vascular fibrous sheath. Where the tubules are cut longitudinally, this differentiation into two muscular coats is well seen. Some of the tubules in

(*b*) show a definite diminution in the muscular coat, which only consists of two or three layers of longitudinally arranged fibres. The rete tubules are exceedingly irregular in shape and extent, the characteristic of the lining epithelial cells being their pale staining reaction. Their shape is cubical—but some of them apparently show a tendency to become flattened. There is no tubular wall apart from the epithelial lining.

Case XVII, age 3 *years.*

A regular cubical epithelium lines the Wolffian tubules, the nuclei being deeply stained. There is a well marked basement membrane. The characteristic inner longitudinal smooth muscle coat is present in all the tubules, but the outer circular coat is thicker and more easily detected in the majority of them, and some of the cells of this coat interlace between those of the inner longitudinal coat. The staining reaction of the muscle cells is normal. There is an outer fibrous vascular coat in all cases.

The rete tubules are not present in this specimen.

Case XV, age 3 *years.*

The epithelial lining of the tubules is cubical in type and resting upon a basement membrane. In one tube of very small lumen, the muscular coat consists of four layers, the usual two coats being surrounded externally by a second series of longitudinal and circular muscle cells (fig. 16). An outer

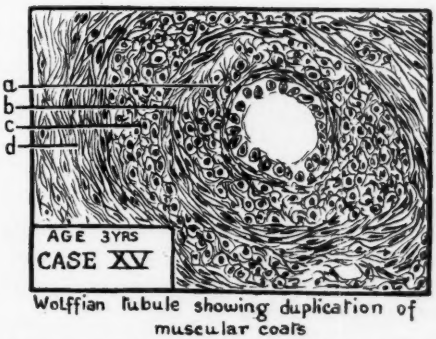

Fig. 16. Microscopical drawing of Wolffian tubule, showing duplication of muscular coats. (*a*) Internal longitudinal coat. (*b*) Internal circular coat. (*c*) External longitudinal coat. (*d*) External circular coat.

vascular fibrous coat is present. In addition to the closely packed arrangement of the muscle fibres, a difference in staining properties is evident, the protoplasm of some of the muscle cells being only faintly eosinophil. This is suggestive of degenerative changes within the cells. The other tubules appear to have a muscular coat consisting of inner longitudinal and outer circular cells.

Case XIX, age 13 *years.*

The Wolffian tubules in block (*c*) are lined by a regular cubical epithelium, resting on a basement membrane, the cytoplasm of the cells being clear and only faintly stained. External to this is the muscular coat, which consists of inner circular, middle longitudinal, and outer circular smooth muscle cells, this last being thick and very well defined in some of the tubules, whereas in others the middle longitudinal coat is the most distinct and thickest. In others, again, the inner circular coat is absent, and the outer circular cells penetrate between the longitudinal cells, which are lying close to the basement membrane. The Wolffian tubules in block (*b*) appear to possess, on the whole, a greater quantity of longitudinal muscle. The rete tubules are again spaces lined by epithelial cells and possess no other wall.

Case V, age 15 *years.*

The Wolffian tubules are lined by a columnar epithelium, with clear protoplasm, placed upon a basement membrane. The muscular coat consists of inner longitudinally arranged smooth muscle cells, which lie touching the basement membrane, and outer circular fibres. The latter partly interlace between the longitudinal fibres, but externally they form a distinct circular coat. The usual vascular, connective tissue coat surrounds the whole tubule.

The rete tubules are even more convoluted than those previously described, and the epithelial lining is distinct, but the tubules still show the elementary structure previously noted.

A small cyst is lined by columnar epithelium, and immediately outside the basement membrane are smooth muscle cells cut through their long axis. The loose connective tissue surrounds the cyst. The wall is very much thinner than that of the tubules seen in the same section.

Case XX, age 23 *years.*

The Wolffian tubules are lined by a regular cubical epithelium, immediately outside which is a longitudinally arranged smooth muscle coat. External to this are circular smooth muscle cells, the majority of which stain normally. There is a vascular, connective tissue sheath.

The rete spaces are very irregular in shape and size and they are lined by a cubical epithelium which varies in the regularity of its arrangement. The cells of this epithelium are placed upon a basement membrane, and possess large, pale staining nuclei, and a quantity of clear, pale cytoplasm. The cytoplasm of some of the cells is finely granular and eosinophil in reaction. In no case is there any definite wall to the tubules, but in certain cases the surrounding dense connective tissue of the hilum of the ovary is more loosely arranged. In other cases the rete tubules have a tubular appearance and are lined by a similar type of epithelium.

Case III, age 24 years.

One tubule seen in block (*c*) is lying surrounded by, but quite separate from, a number of large blood vessels. The epithelial lining consists for the most part of one layer of cubical epithelial cells, but this layer is reduplicated at one point, probably due to oblique cutting. The basement membrane is very incomplete. Outside this is a zone of homogeneous eosinophil staining material, and Mallory's stain shows this to be white fibrous connective tissue (fig. 17).

The muscular coat again consists of two layers of muscle cells—an increased number of which show the pale staining reaction previously noted. Moreover, interlacing between the cells of both muscular coats can be seen connective

Fig. 17. Microscopical drawing of Wolffian tubule, showing degenerative changes.
(*a*) Epithelium. (*b*) White fibrous connective tissue.
(*c*) Smooth muscle cells, with very pale staining reaction.

tissue fibres from the inner fibrous layer. The outer vascular sheath is scanty in amount. Tracing the tubule through its adjacent sections, the lumen is found to be large and distinct, and the histological structure uniform in thirteen of them. In the 14th section, however, the blind end of the tubule is reached, and in the following sections, the closed in muscular wall is seen.

Other tubules noted in block (*c*) are much smaller, and show a variety in size and shape of the lumen, evidently due to a very tortuous course. The histological structure, however, is similar to that described above.

Case IV, age 29 years.

The whole of the tissue is infiltrated by masses of small round cells, but the histology of the embryonic tubules does not seem to have been affected by this.

The epithelial lining consists of a single layer of cubical cells. In many of the tubules the cells have been broken away from the basement membrane. The muscular wall of the tube consists of circular and longitudinal muscle cells, showing no definite arrangement. In fact, the whole tissue structure seems much less compact than in previous cases.

Case VIII, age 36 years.

The tubules in block (*c*) show certain variations in structure, being lined, some with a flattened epithelium, and others with a cubical epithelium, resting on a basement membrane. The muscular wall lying adjacent to the latter, shows the usual internal longitudinal and external circular coats. A vascular connective tissue coat is present.

Other tubules show a well-defined cubical epithelium, placed on an incomplete basement membrane. The wall consists of an internal circular muscle layer, the staining reaction of most of the cells being normal. Outside this are seen a few longitudinally placed muscle cells, with a poor affinity for eosin, external to which is an outer circular muscle coat.

The duct seen in block (*d*) shows a well-defined cubical epithelial lining, the nuclei and cytoplasm of the cells staining deeply. This, in places, has become detached from the wall of the duct.

The wall is thin, and the region next to the epithelium appears to consist of densely packed connective tissue cells. Surrounding it and penetrating it are bands of smooth muscle cells, derived from the uterine wall.

Case XXII, age 43 years.

The Wolffian tubules are lined by a regular cubical epithelium, resting on a basement membrane, the nuclei of the cells staining deeply with basic dyes, and the protoplasm being markedly granular and eosinophil. Immediately external to the basement membrane is a longitudinal smooth muscle coat, which is very clearly shown in a longitudinal section of one of the tubules, and outside this is a circular muscle coat, the whole tubule being surrounded by a vascular fibrous sheath.

The rete tubules seen in the hilum of the ovary are very irregular in shape, and are lined by a single layer of cubical epithelial cells, which stain deeply. No wall can be said to exist, and there appears to have been no rearrangement of the tissues in the vicinity to form a support for the tubules.

Case XI, age 50 years.

The Wolffian tubules are lined by cubical epithelial cells resting on a basement membrane, external to which are a few degenerating smooth muscle cells, arranged longitudinally, interlacing between which is fibrous connective tissue, which thus forms most of the wall of the tubule. There are few blood vessels in relation with the wall of the tube. Other tubules show a greater amount of muscle, and a marked occlusion of the lumen has not been noted.

The rete tubules are irregular spaces, lined by a cubical epithelium, but otherwise devoid of a definite wall (fig. 18).

Case XIII, age 50 years.

The tubules in block (*b*) are cut obliquely, so that the cubical epithelial lining appears to be more than one layer thick. But the structure is the same as of those about to be described.

The whole structure seems to have enlarged in proportion to the growth of the surrounding tissues. The epithelial lining of the Wolffian tubules rests

Fig. 18. Microscopical drawing of rete tubules, which consist of irregular spaces lined by epithelium, but devoid of definite wall.

on a basement membrane, and the muscular wall shows two layers—inner longitudinal and outer circular. The cells stain faintly and present a loosely packed appearance.

The rete tubules are lined by a columnar epithelium, and are again highly irregular in shape. The epithelium is immediately surrounded by loose connective tissue, external to which is the fibrous tissue of the hilum of the ovary.

Case XXI, age 51 *years.*

The rete tubules appear in many of the sections as irregular clefts lined by cubical epithelium, the nuclei of the cells staining very deeply. In other sections, the spaces assume a more tubular appearance. Surrounding the tubules are strands of closely packed white connective tissue fibres running in all directions, between which are seen more loosely arranged fibres. A number of small blood vessels is seen amongst the fibres. The Wolffian tubules are lined by cubical epithelium, resting upon a basement membrane, external to which is a coat of longitudinally arranged smooth muscle cells, the nuclei of which are well stained, but the cytoplasm stains badly in some of the cells. Outside this is a circularly arranged muscle coat, interlacing between the cells of which are delicate white connective tissue fibres. In some cases a second longitudinal coat is seen outside the circular coat, but this is not universal. There is an outer vascular fibrous coat.

Case VI, age 65 *years.*

Several Wolffian tubules are lined by cubical epithelium, but seem to possess no tissue coats. This appearance is maintained in a number of sections. Round the epithelial lined tube is disposed the connective tissue and smooth muscle of the mesosalpinx. Probably the existence of the tubule causes this local arrangement. No degenerating muscle fibres are seen.

In other cases, the lining consists of cubical epithelium on a basement

membrane, lying embedded in a tissue rich in smooth muscle cells. In most of them it is impossible to distinguish a longitudinal coat outside the epithelial cells, but apart from this the muscle seems to be cut in all planes, thus suggesting a highly convoluted course of the tubes. Moreover, the muscular walls of adjacent tubules seem to be continuous one with the other.

The junctional or rete tubules are here represented by minute regular tubes, lined by cubical or columnar epithelium and invested in a thick sheath of loose connective tissue.

The duct of Gärtner is lined by a single layer of cubical epithelial cells of extreme regularity in arrangement. In only one part is the epithelium reduplicated. The nuclei are well stained and are placed at the bases of the cells. There is a fair amount of eosinophil granular protoplasm, and a distinct basement membrane is visible. The wall is composed of smooth muscle fibres cut longitudinally, being of the thickness of about four fibres. Outside this well marked muscular wall is a small amount of connective tissue in which a thin walled blood vessel is seen.

PART V. SUMMARY AND CONCLUSIONS

Occurrence

Gross anatomical dissection of the mesosalpinx revealed the presence of the Wolffian body, consisting of horizontal duct and vertical tubules, in every case out of a total of fifteen specimens dissected. Microscopic examination of serial sections confirmed this in nineteen cases out of a total of twenty examined, the reason for failure to find the Wolffian body on one side in the twentieth case being the rejection of that part of the mesosalpinx lying lateral to the ovary. In no case has it been possible, by either method, to demonstrate the presence of the paroophoron apart from the Wolffian body, and this is in direct contradistinction to the findings of Rielander (18). In two cases only, out of a total of eighteen, has the presence of Gärtner's duct been detected, and in each, the extent of the duct was limited to a microscopic length. It has been possible to demonstrate by histological methods the presence of the rete or junctional tubules of Allen (1) in thirteen cases out of a total of seventeen, the reason for the diminution in the total number of cases being the fact that a number had been examined and a valuable part of the mesovarium and hilum of the ovary cut away before these elements were detected in one of the specimens. As far as I am aware, this is the first time that the rete tubules have been demonstrated in the human female, though their presence has been suspected and their anatomical position described as being close to the ovarium fimbria (13). Coblenz (5) detected relics of the Wolffian tubules in the tissue of the hilum of the ovary as long ago as 1882, and possibly he was then describing the rete tubules.

Distribution

The accompanying table (Table II), based upon the microscopical findings, explains the distribution of the embryonic remains throughout the broad

ligament (figs. 7 to 13). The dissected specimens show that the actual position of the Wolffian body depends to some extent upon the method of pinning out the fresh specimen before fixation. Thus the distribution of the Wolffian body is very variable, but it has not been found to extend nearer to the uterus than the uterine pole of the ovary. The rete or junctional tubules are fixed by the attachment of the mesovarium to the hilum of the ovary, and have not been found to migrate from this position, although there has been a variation in the distribution of these tubules in different specimens. In some, they extend throughout the whole of the hilum of the ovary or mesovarium, in others they disappear for a short distance and then reappear. J. L. Bremer (4) finds that the rete cords in the male foetus form a network, and that the boundary line between the rete network and the testis tubule network is wavy and irregular. Possibly this accounts for the fact that in some cases the rete tubules have been found in the hilum of the ovary, and in others in the mesovarium.

Growth

In my series of cases, ranging from the 8th month of foetal life to the age of 65 years, the Wolffian body was of largest size and showed the greatest number of tubules in a subject aged 50 years. On the other hand, where two or three specimens of the same age were examined, a difference in the degree of development in each case was found (for example, in another case of 50 years the Wolffian body was less well developed than in one of 13 years), so that it is impossible to give an age of maximum development upon so small a series of cases (compare Cole (6) and Keith (13)). It is to be noted that seven of my specimens out of a total of fifteen examined with the naked eye showed the presence of eight vertical tubules in the Wolffian body. Yet one case had thirteen tubules, and another case ten tubules, and the question arises—do the tubules increase in number after birth, during the development of the generative organs, or are some of the tubules so small at an early age, that they are not detected by the unaided eye? Microscopical examination does not throw any light on this question, as the number of tubules counted cannot be an accurate index of the number present, one tubule being cut many or several times in the same section. It would be necessary to reconstruct the Wolffian body to prove this point.

Histology

The typical histological structure of a Wolffian tubule is a cylindrical tube lined by a single layer of regular, cubical epithelial cells, resting upon a basement membrane, and immediately adjacent to a longitudinal smooth muscle coat, external to which is a circular muscle coat. A vascular fibrous connective tissue sheath surrounds the whole (compare Piersol (17)). In no case have I found the epithelium to be ciliated (compare Eden and Lockyer (9)). The Wolffian duct can be rarely recognised as a distinct structure, but where

present it has been detected by the larger size of its lumen, and the increased thickness of its muscular coats.

Note on Morphology

This presence of an inner longitudinal muscle coat suggests at once an analogy with the structure of the ureter (19) which possesses inner longitudinal and outer circular muscle coats. When one considers that both the Wolffian duct and the ureter are outgrowths from the allantois or primitive bladder (12), this similarity of structure is suggestive and interesting. The mesonephric tubules are developed as secretory kidney tubules, and therefore consist of glomerulus, tubule proper and peritoneal funnel, though according to Keibel and Mall (11) they do not function as such in the human embryo. In the male, they acquire the function of conducting the spermatozoa from the seminiferous tubules of the testis to the duct or collecting tube, which becomes the vas deferens. In the female they appear not to function at any period. Yet they are found histologically to possess those muscular coats which the cavity, from which they develop as an outgrowth, possesses.

Histology (*contd.*)

The changes in the histology of the Wolffian body tubules, which occur as growth proceeds, appear to be twofold:

1. A degeneration of the muscular coats, evidenced by failure on the part of the cells to stain with various reagents. This is followed in some cases by an ingrowth of muscle from surrounding tissues.
2. A replacement of the muscular coats by white fibrous connective tissue, which interlaces between the few remaining smooth muscle cells.

This is contrary to Cole's statement (6) that as age advances the tubules are converted into solid cords of fibrous tissue in which are blood vessels. I have found that the epithelial lining can always be detected, although, as stated by Alban Doran (8), with increasing age the epithelial cells show a tendency to be cast off from the wall of the tube and to lie loose within the lumen.

The rete or junctional tubules of Allen (1) are very uniform in structure and show little variation in histological appearance as the age of the specimen increases. The epithelial lining of cubical cells in every case is devoid of the support of a muscular or fibrous wall. The spaces rarely assume a tubular character, but exist as irregular spaces lying amongst the dense connective tissue of the hilum of the ovary or mesovarium. It is significant that no case has been observed of dilatation of these tubules, which might suggest the beginnings of cyst formation. On the other hand, it seems probable that any cyst containing smooth muscle cells within its wall cannot originate from these rudiments, as in only one case (XIV) has muscle been observed in relation with them, and even in this specimen the arrangement of the muscle

fibres suggests that they have only approached the tubules from surrounding tissues.

Criticism of Technique and Suggestions for Future Investigations

This investigation is not yet complete, and certain points in technique have been clearly demonstrated as the work has proceeded.

1. The microscopical examination of block (*a*) (fig. 1) has in every case yielded a negative result, so that this tedious procedure might be omitted.

2. Certain landmarks, such as the Fallopian tube, with its fimbriae, should be left intact to assist in accurate orientation.

3. Where the ovary is too large to embed in one piece, the portion not required should be carefully cut away, so as to leave the rete tubules, which may extend into the ovarian tissue. Also, the attachment of the mesovarium to the mesosalpinx should be left intact.

4. Microscopical examination of block (*d*) (fig. 1) is the most difficult problem. The length of the tissue may be $2\frac{1}{2}$ inches—which necessitates the cutting of an enormous number of sections even at a thickness of 20μ. Yet this procedure is safer and more accurate than dividing the block into pieces (usually three) and cutting only 200 sections from each block.

5. A reconstruction of the Wolffian body and rete tubules would be invaluable, and this should be undertaken from a young adult specimen, where no pelvic abnormalities are present.

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THE INTERCHONDRAL JOINTS OF THE HUMAN THORAX

By SIR CHARLTON BRISCOE, Bt.

With the view of elucidating the mechanism of respiration I have examined one hundred specimens of the sternum and attached cartilages obtained from the post-mortem room. The attachments of the triangularis sterni and of the diaphragm together with the interchondral joints were carefully investigated and recorded. The characteristics of, the variations exhibited by, and the movements occurring in the interchondral joints are the main theme of this paper.

The costal cartilages between which interchondral joints may exist are the 5th, 6th, 7th, 8th and 9th. No joint between the 9th and 10th costal cartilages was ever found, the connection between the two being always in the form of loose connective tissue or muscle. A joint between the 4th and 5th costal cartilages was met with in one case only. It was unilateral, being situated on the left side and must be a rare condition. It may be taken as a general rule that the more cephalad the interchondral joint the nearer it is to the middle line.

Between the adjacent cartilages from the 5th to the 9th there may exist (*a*) synovial joints, (*b*) ligamentous union without a joint cavity, (*c*) direct cartilaginous union, (*d*) connection by means of muscular or loose connective tissue. When a synovial cavity exists a wedge-shaped spur usually extends downwards from the higher cartilage to meet the lower cartilage. The thickest and best marked spurs are found between the 7th and 8th cartilages. The spur is flush with the ventral surfaces of the two approximated cartilages, but lies in a plane anterior to their deep surfaces. The deep surface of the spur may be covered by a few fibres of the intercostal musculature, which is always absent on its superficial surface. The articular facet on the spur is flat or slightly convex, it looks downwards and slightly forwards. The corresponding facet on the cartilage below is either flat or slightly concave and looks upwards and slightly backwards. The lower facet may be flush with the upper aspect of the cartilage on which it is present. Sometimes, however, it is depressed, on the other hand, it may occupy an elevation.

The synovial cavities extend from $\frac{1}{4}$ to 1 inch or more in the long axes of the cartilages between which they lie. The longer and more extensive joint cavities are found in cases where the successive cartilages are more or less closely approximated and spurs between adjacent cartilages are not well marked. An interchondral synovial joint is surrounded by a dense ligamentous capsule whereby the movements are strictly limited.

When no synovial cavity is present the cartilages may be bound together by a fibrous band. A spur may project downwards from the upper cartilage. This spur may have no special connection with the lower cartilage or may be attached to it by a fibrous band.

Cartilaginous union between successive costal cartilages occurs as frequently in children as in adults, and for this reason I do not regard the condition as secondary.

The incidence of these joints is shown in the following table.

	Right						Left					
Between	Number examined	Synovial Joint	Fibrous Union	Cartilaginous Union	Spur	Percentage with Synovial Joint	Number examined	Synovial Joint	Fibrous Union	Cartilaginous Union	Spur	Percentage with Synovial Joint
9th and 8th cartilages	44	8	29	7	—	18 %	46	13	28	5	—	28 %
8th and 7th cartilages	96	71	15	10	—	74 %	95	84	5	6	—	88 %
7th and 6th cartilages	100	92	0	7	—	92 %	100	92	3	4	—	92 %
6th and 5th cartilages	100	46	1	—	10	46 %	100	22	—	—	17	22 %

From a study of the table it is apparent that synovial joints between the 6th and 7th costal cartilages are equally prevalent on the two sides of the body. Interchondral synovial joints between the 7th and 8th and between the 8th and 9th are more frequent on the left side than on the right. On the other hand synovial joints between the 5th and 6th costal cartilages are twice as numerous on the right side as they are on the left. If, however, the presence of a spur be regarded as an indication of a synovial joint having existed in earlier life the proportion between right and left side, as regards the presence of a synovial cavity, may be taken as 56 per cent. to 41 per cent.

The movements at the interchondral joints are of two kinds: (1) antero-posterior, the lower cartilage moving forwards and backwards on the upper, the former undergoing a greater amount of rotation than the latter, the antero-posterior diameter of the chest being increased or diminished thereby; (2) a gliding movement in the direction of the long axes of the two cartilages which increases or diminishes the transverse diameter of the chest.

Antero-posterior movement occurs in over 80 per cent. of any of these joints and is more marked in the higher joints than in the lower. Gliding movement occurs in 70 per cent. of specimens between the 8th and 9th cartilages. Between the 5th and 6th, and 7th and 8th cartilages gliding movement occurs in approximately 60 per cent., between the 7th and 8th cartilages in 30 per cent. The joint between the 7th and 8th cartilage is the least mobile in either direction and on either side. The highest joint in the series exhibits the greatest mobility and appears to act as a fulcrum for the lower cartilages.

The chief interest of these observations seems to lie in the presence or absence of synovial joints between the 5th and 6th costal cartilages and the tendency for such joints to diminish in number with advancing years.

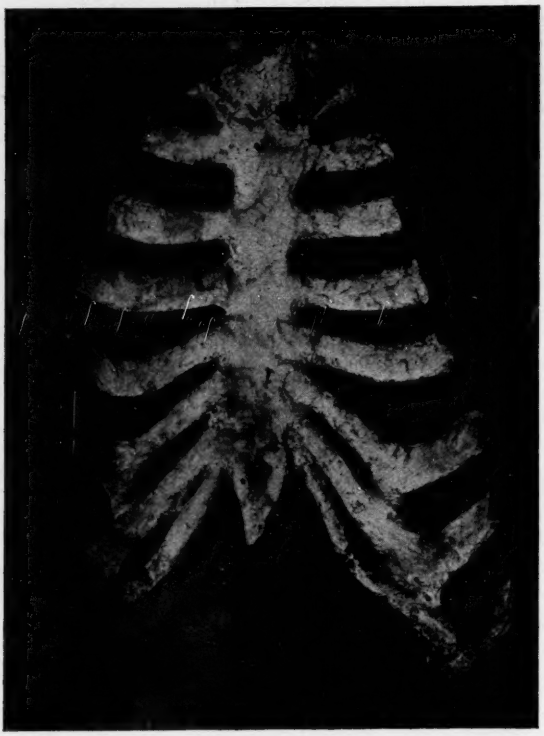


Fig. 1. Sternum and costal cartilages from a male aged 43 years viewed from behind. A synovial joint between the 6th and 7th costal cartilages is present on both sides. There is no joint between the 5th and 6th costal cartilages which are separated from one another by comparatively wide intervals. The 8th costal cartilage reaches the sternum on either side.

The specimens may be divided into three groups, the constituent numbers of which are nearly equal.

Group 1. Under 10 years of age ... ... 31 cases.
„ 2. From 10 to 50 years of age ... ... 34 „
„ 3. Over 50 years of age ... ... 35 „

The percentage of specimens showing a synovial joint between the 5th and 6th cartilages is:

Group 1, on the right side 56 %; on the left 28 %.
„ 2, „ „ 50 „ „ 22
„ 3, „ „ 35 „ „ 21

If the presence of a spur be taken as evidence of the existence of a joint in earlier years, the figures are:

Group 1, on the right side 74 %; on the left 54 %.
„ 2, „ „ 55 „ „ 35
„ 3, „ „ 42 „ „ 28

The decline in the number of joints in older life runs *pari passu* with the disappearance of the spurs.

The type of breathing in a child at birth is chiefly costal. The diaphragmatic type of breathing becomes accentuated when the child begins to assume the upright position. This change is progressive through adult life and the diaphragmatic type is the more pronounced when calcification of cartilages

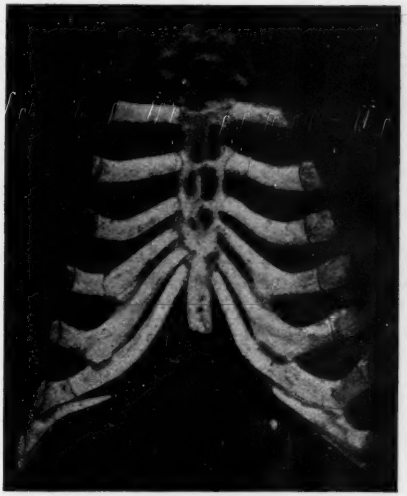


Fig. 2. Sternum and costal cartilages from a male aged 5 months viewed from behind. A synovial joint between the 5th and 6th costal cartilages is present on both sides.

limits chest expansion above the age of 50. In early days any formation which assists thoracic expansion is an advantage and these joints will do so by facilitating the increase of both the antero-posterior and transverse diameters of the lower part of the chest. With the advent of abdominal breathing the importance of this action is diminished. A corresponding change occurs in the size of the epigastric angle formed by the lowest rib cartilages articulating with the sternum. Up to two years of age this measures more than 75°, after three years of age more than 50 per cent. of cases show an angle less than 75°. (There is, however, no relationship between the presence of joints between the 5th and 6th costal cartilages and the size of this angle.) The narrower the epigastric angle the greater is the tendency to the diaphragmatic type of breathing.

The sexes of the individuals from whom the specimens were obtained was recorded in 77 instances, 23 females, 54 males.

Considering the joints between the 5th and 6th cartilages only. In females, 8 specimens show a synovial joint on the left side (34 per cent.), 14 specimens show a similar joint on the right side (61 per cent.). In males, 9 specimens show a synovial joint on the left side (16 per cent.) and a similar joint on the right side in 22 cases (49 per cent.). There is, therefore, a marked preponderance of synovial joints between these cartilages in the females, as compared with the males.

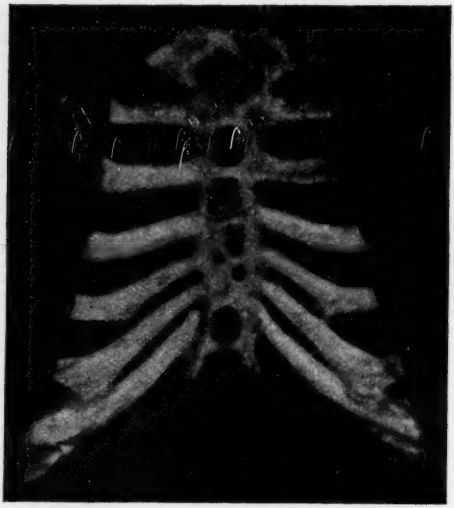


Fig. 3. Sternum and costal cartilages from a female aged 1 year 10 months viewed from behind. A synovial joint between the 5th and 6th costal cartilages is present on the right side but is absent on the left side where a spur of the 5th costal cartilage extends downwards and approaches but does not meet the 6th costal cartilage.

An explanation of these figures may be found in the effect of pregnancy on the type of breathing, as in the later months respiration tends to become markedly costal.

Concerning the action of the diaphragm on the rib cartilages it may be pointed out that the first part of the muscle to contract is the crus. By means of the central tendon and the part of the diaphragm attached anteriorly, the direct line of pull of the crus affects the 7th and 8th costal cartilages—and tends to pull these cartilages backwards towards the vertebral column. Such recession occurs only in dyspnoea, and is not found in quiet breathing. The forward movement of these cartilages must therefore be effected by other means, viz. by the intercostal muscles.

Keith (*Anat. Soc.* May 1903, "Contributions to the human mechanism of respiration") states that neither facets nor spurs nor direct contact between cartilages are found in pronogrades. "In the anthropoids the 6th, 7th and 8th come together and synovial facets are found, but the great heels of cartilage which are thrown out at these articulations are found only in the human thorax."

He accepts H. von Myers' explanation "that through these inter-articulations the diaphragm may exert its lifting force on the ribs above those to which it is attached."

I think that the points against this view, in addition to those mentioned above, are:

1. The pronogrades breathe chiefly with the diaphragm and have no such intercartilaginous joints.

2. The upper chest in man in quiet respiration is expanded and raised by the intercostals and scalenes which can be felt to contract in every individual at rest and tracings show some movements in everyone. There is ample provision for this elevation without invoking the aid of the diaphragm.

3. Where diaphragmatic descent in respiration is well marked the transversalis between the 7th, 8th and 9th cartilages contracts during inspiration and prevents eversion of these ribs in the mid-axillary line. The lower intercostals often contract in expiration and approximate the ribs. This is not in accord with the view that the diaphragm elevates the chest.

In prolonged supine posture, in late pregnancy, in paralysis of one phrenic nerve, in hysteria and asthma respiration becomes markedly thoracic. In this type of breathing the eversion of the mid-axillary line is more marked over the 7th and 8th ribs than elsewhere, and generally more on the right side than on the left. The right side is more richly provided with intercartilaginous joints.

This numerical preponderance is probably due to the presence of the liver on the right side which must be a constant factor preventing the lower ribs inverting to the full. On the left side the stomach can only act intermittently in this manner.

The conclusion therefore is that the intercartilaginous joints assist in the expansion of the lower thorax, not in the elevation of the upper ribs and that such expansion is effected by the action of the intercostal muscles and not by the diaphragm.

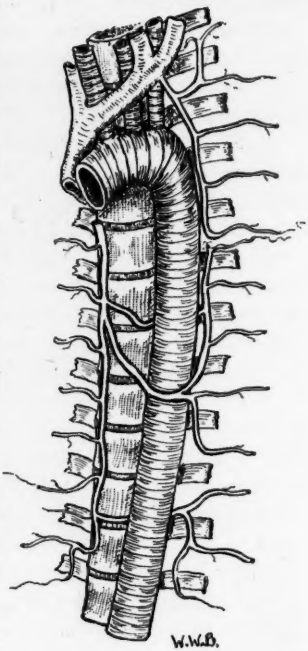
AN ABNORMAL VENA HEMIAZYGOS

By H. C. LINDSAY

Student in Anatomy, Queen's University, Belfast

Variations in the number and arrangement of the hemiazygos veins are very common. Descriptions of the more frequent of them are to be found in the text-books and a careful analysis of the conditions in thirty-two subjects is given in the *Journal of Anatomy*, vol. xxx, p. 197.

The variation I have to describe occurred in an adult female subject. The intercostal veins of the upper five spaces of the left side were drained by a common trunk which was completed in the second space but terminated as the supreme intercostal vein in the innominate vein; there are represented in this trunk, therefore, the posterior cardinal and supracardinal veins. The veins of the lower two spaces (tenth and eleventh) and the subcostal vein were very small; they opened into a small inferior hemiazygos vein which passed posterior to the aorta and the thoracic duct and opened into the azygos vein. There is represented in it, in a typical way, part of the supracardinal vein. The veins of the sixth, seventh, eighth and ninth spaces joined a common trunk which passed obliquely to the right side at the level of the eighth vertebra *in front* of the aorta and *behind* the thoracic duct to end in the azygos vein; and from the upper end of the trunk there was a small post-aortic transverse branch which was joined by a twig from the fifth space.



A pre-aortic transverse anastomosis is one of the rarer types of variation of the hemiazygos veins. One instance of it, associated with a pre-aortic course of the thoracic duct, was described recently by Hafferl[1] and he refers to but one other example (by Krause) to be found in the literature; there is, however, a reference to one instance in the analysis in the *Journal of Anatomy* cited above. A pre-aortic anastomosis between the supracardinal systems is not figured by Huntingdon and McClure in their memoir on the development of these veins[2]; whether these recorded instances represent the persistence of such an anastomosis or whether they belong to the oesophageal venous plexus it is not possible now to decide.

I have to thank my fellow student, Mr W. W. Bassett, for the drawing of the specimen.

[1] "Ein Fall v. abnormem Verlauf d. Ductus thoracicus u. d. Vena hemiazygos," *Anat. Anz.* Bd. LVII. S. 373. 1924.

[2] "Development of the veins in the cat." *Anat. Rec.* vol. XX. p. 1.

AN OS INTERFRONTALE

By EDITH F. WILLOCK, M.B.

The following instance of a large os interfrontale, present in a living male infant of two and a half months, is of interest.

The metopic suture in this case was widely open and the interfrontal bone was situated in the resultant interval between the frontal bones, and extended upwards into the anterior fontanelle. The bone was leaf shaped, closely resembling the epiglottis in outline and its narrow inferior extremity could be traced to the angle of union of the frontal bones, 1·5 cm. from the nasion, and appeared to be united to them at this point; the superior extremity encroached on the anterior fontanelle, but did not extend as high as the line of the coronal suture. The bone measured 4·5 cm. in length and its maximum width, approximately at the juncture of the upper and middle thirds of its long axis, was 2 cm.

An X-ray photograph showed this bone to be circular in shape and entirely separated from the frontal bones, but this appearance was due in all probability to its incomplete ossification: there was no evidence of more than one centre of ossification.

The anterior fontanelle was large, the distance from its posterior angle to the superior extremity of the os interfrontale being 5 cm. while its maximum width was 6 cm. and the width at the upper limit of the interfrontale bone was 3 cm.

The skull was slightly dolichocephalic (cranial index 74·3) and was cryptozygous. The lamboid suture was open and a definite space intervened between the margins of the occipital and parietal bones; this was most marked on the left side and was confirmed by the X-ray picture. The X-ray also showed that the margins of the coronal suture on the right side were not in apposition. In other respects the skull appeared normal and there was no evidence of hydrocephalus.

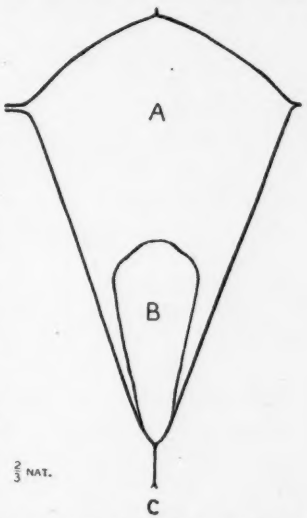


Fig. 1. Diagram of anterior fontanelle and interfrontale bone, drawn to scale. *A*, anterior fontanelle; *B*, interfrontal bone; *C*, nasion.

The infant, which was admitted to the Manchester Babies' Hospital as a severe case of marasmus, was very wasted on admission but improved slowly under prolonged treatment. The eyes

somewhat approached the Mongolian type and both lower lids showed a slight degree of entropion. Both ears were malformed as regards the helix, antihelix and antitragus. Pulmonary, cardiac and abdominal examination revealed nothing abnormal. No family history of importance was obtainable and there were no brothers or sisters.

Le Double (*Traité des variations des os du crâne de l'homme*, Paris, 1903) has collected the literature on the subject of interfrontal bones and has added

Fig. 2. To illustrate the position of the interfrontal bone. (A photograph of the skull of an infant on which has been painted the outline of the anterior fontanelle and interfrontal bone as in the case described.)

to this the result of his own series of cases. He states that there are three types of os interfrontale: (1) the os nasofrontale, situated in the region of the nasion; (2) the os médiofrontale or métopique, which lies in the metopic suture at the juncture of its middle and lower thirds (Staderini, quoted by Le Double, found this type to be present in ·3 per cent. of his series); (3) the os bregmatique, situated in the region of the bregma, which was found in ·6 per cent. of all skulls examined. The os bregmatique possesses many other synonyms, varies widely in size and shape, and attains to greater dimensions than either of the other two types. According to Le Double, this bone may be divided horizontally in the plane of the coronal suture and either portion

may exist alone; should the bone lie below the coronal plane it is termed infrabregmatique (interfrontal), if above, suprabregmatique (interparietal).

Wormian bones are frequently associated with the presence of hydrocephalus and in this case the possibility of the latter condition was suggested by the state of some of the sutures; there was, however, no hypertension of the fontanelle and no other signs or symptoms were present, so its absence was presumed.

There is some doubt as to which class of interfrontal bone this case should belong. Its large size is in favour of its being considered an os hémibregmatique (infrabregmatique), and at first sight the X-ray findings support this view, as the only ossified area shown is in the region of the upper extremity of the bone. Clinically, however, the bone is in intimate relation with the metopic suture and is apparently united at a low level, 1·5 cm. from the nasion, with the frontal bones, while its upper extremity barely reaches the position of the anterior angle of a normal fontanelle. Remembering that the X-rays merely show the existing area of ossification and are no true criterion of the actual extent of the bone, the evidence would seem to indicate that this case is in reality one of an os métopique of exceptionally large dimensions.

I am indebted to Dr Catherine Chisholm for permission to publish this case.

ANATOMICAL MANIKINS[1]

By C. J. S. THOMPSON, M.B.E.
Curator of the Wellcome Historical Medical Museum

The Chinese appear to have been the first to have employed anatomical manikins, not only for instructing students in the structure of the body as known to them, but also for teaching the art and practice of acupuncture. There are several of these manikins in the Wellcome Historical Medical Museum which are of considerable antiquity. One is a bronze figure 33 cm. in length, the head, body and limbs of which are perforated with ninety small holes in certain places to show where the acupuncture needles should be inserted in the treatment of various diseases. It is said to be of the fourteenth or fifteenth century.

An interesting Chinese manikin is carved in dark wood and probably dates from the early sixteenth century; it represents the head and body, and is 8·50 cm. in length. The internal organs shown are the lungs and liver, which are carved in a flower-like form common in Chinese anatomical drawings of this period; the heart is carved out of the solid, and the colon, intestines, kidneys and bladder are also shown. The spinal column is fashioned in detail.

Another of these manikins represents the figure of a man carved in ivory 9 cm. in height, and probably dates from the late fifteenth century. The body is divided into two parts by a line from the crown of the head to the feet. The right side is graved with straight and curved lines with ideographs in certain places, indicating the parts of the body for the insertion of the acupuncture needles.

In Europe ivory anatomical manikins were known from the early part of the seventeenth century. The first met with represents a female figure in a recumbent position 15 cm. in length, mounted on an ebonised base. The arms are movable, and hinged to the body with wooden pegs. The upper part of the body is made to open, and when lifted discloses the viscera with movable models of the intestines, uterus and kidneys, which in this particular specimen are imperfect; the other internal organs are missing.

Some of these anatomical manikins are found in pairs representing male and female. The following pair are larger than the former specimen, and measure 16 cm. in length. Each is mounted on a wooden block in the shape of a bier covered with old crimson silk velvet; the heads rest on a square pillow carved in ivory, with a pierced border to imitate lace. The internal organs in these manikins are more complete, the male having the liver,

[1] Abstract of a paper read before the History of Medicine Section of the Royal Society of Medicine.

stomach, kidneys and part of the heart, and the female the foetus in utero and the lungs in addition to the former organs.

In the collection of these manikins now in the Wellcome Historical Medical Museum, some are mounted on biers covered with silk or velvet, while others are enclosed in stamped leather cases, lined with silk or soft leather, for the purpose of being carried about. They probably date from the early seventeenth to the eighteenth century, and from a careful comparison of the workmanship of the carving with other ivories I have come to the conclusion that some were made in France and others in Italy. It is probable that they were the work of the craftsmen who carved the figures of Christ that are to be found on the crucifixes of the time. On studying the various features of these manikins they will be found to fall into two distinct groups. First, those in which the head of the male represents that of an old man, with attenuated features and a grave expression; the arms, legs and removable parts being well executed, while the corresponding female manikin has the hair drawn back from the forehead. The head is usually small in proportion to the body, but otherwise the carving and modelling is good.

The second group of manikins have distinct features and are quite Italian in character. The heads of the males are larger and broader and they are usually represented with long hair and heavy curling moustaches. The carving of the Italian figures is not so artistic and is cruder than those I believe to be of French origin. The female manikins of the Italian type are often represented smiling; the hair is brushed back, and confined by a bandeau, while the features have distinct characteristics and are quite different from the French type. In some of these specimens the arms are movable, being attached to the shoulders by wooden pegs, in others they are rigid, and joined to the body. In all the specimens the upper part of the trunk may be lifted off, disclosing the viscera. The modelling of the organs varies very considerably in these figures, and seems to have been largely left to the ideas of the carver. Some are very conventional, while others are more natural. Veins and arteries are drawn in colour, and in some of the manikins the liver, heart and other organs are stained red. In every case the intestines are removable, and beneath, in the male figures, is found the bladder, and in the female the foetus in utero, the cord being represented by a red silk thread.

Perhaps the most interesting pair of these ivory manikins, male and female, are enclosed in a beautifully stamped brown leather case of the seventeenth century. It is lined with an old French paper decorated with a design in various colours, resembling the petals of flowers. The figures, which measure 20 cm. in length, recline on beds covered with blue silk edged with gold braid. The heads rest on blue silk cushions bordered with gold braid, and have pieces of pink ribbon at the corners. The position of the arms in these specimens is different from the others, the right arm being carved out of the solid ivory and extended down the right side, while the left is also straight, but movable from the shoulder. The viscera of the male figure is divided into two parts

by a kind of shelf representing the diaphragm. In the upper part are models of the heart, suspended by pink silk thread, and the lungs. Below the diaphragm there is the stomach, kidneys, descending aorta and the bladder. An attempt has been made at drapery over the left thigh in this model, which is unusual in these figures. The female figure is rather longer, and measures 20·50 cm. in length. The left arm is carved in the solid and joins the body, while the right is movable. The viscera is divided in the same manner as in that of the male figure, but the internal organs are better modelled; the heart is enclosed by the lungs, which are hinged with pink silk. Below the diaphragm the stomach, kidneys, bladder and uterus are all represented. Veins and arteries are painted in thin red lines, and the foetus is well carved, the cord being represented by red silk thread.

Another pair of these ivory manikins worth describing is the most perfect in the collection, and I believe are of Italian workmanship. Each figure fits into a separate case measuring 26 cm. by 10 cm., the outsides being covered with old leather. The insides and lids are lined with chamois leather stained red and edged with gold braid. The male figure is mounted on a loose bier covered with old blue silk with a pattern of flowers, and decorated with tinsel in squares. The heads rest upon ivory pillows with borders carved to represent lace. The face of the male manikin is of the Italian type, broad, with flowing moustaches, the hair being long and brushed back from the forehead. Both arms are movable from the shoulder, and in the cavity practically all the organs are indicated, some being coloured red, while the veins are shown by red lines. The heart is well modelled, the lungs being kept in position by two pieces of thin red silk and the intestines are covered with an apron of membrane. The internal organs of the female manikin are coloured in the same manner, and although conventionally represented, they are well modelled. In this specimen an attempt has been made to show the pancreas and colon; the uterus is large, and contains the foetus in a normal position, to which is attached a thin red cord. The bier on which the female manikin reclines is covered with red silk which is perforated with small diamond shaped holes, with a blue silk edging. The head is raised, and the face is represented smiling, with the eyes closed; the hair is brushed back, and round the forehead is a bandeau.

The most remarkable manikin in the collection is one representing a woman, carved in marble. It measures 19·50 cm. in length, and is mounted on a wooden bier or table with four legs 7·50 cm. high, 20 cm. long and 5·50 cm. wide. The table is covered with a pall made of tin, coloured crimson, with a gold edging resembling braid. The head rests on a marble pillow, but the face is unlike any of the other specimens, the hair being parted in the centre and falling to the shoulders on each side of the head. The arms are movable, the left being slightly bent, while the right is flexed and rests on the abdomen. The internal organs are carved in marble and movable; an attempt has been made to represent the sternum and ribs, on removing which the heart and

Ivory Anatomical Manikins, Male and Female, 17th century, probably Italian.

lungs are disclosed. A small foetus carved in marble with a silk cord attached is fitted into the uterus, over which lie the intestines.

The question has often been asked, why were these manikins made, and for what purpose were they employed. Some believe they were made simply as models of human anatomy, and like the Anatomical Fugitive Sheets, were fashioned for the curious and not for purposes of instruction. The problem would have been difficult to solve had it not been for a document which was found by Dr Capparoni in a case containing one of the manikins which supplies us with an answer beyond conjecture. The script is in old French, of which the following is a translation:

In Life's full bloom, when labour's toil so near
My fellow sufferers' lot and perils I do fear,
Come ye fair pupils, Lo, I cast aside my shame
That Midwif'ries secrets may reveal my frame.
Pierce it with keen enquiring eye, and may
The child and mother's nature then convey
New manifold devices to your skillful art
That pining women may not henceforth smart
Through cruel untaught efforts, and not gasp
With their unborn in Death's unpitying grasp.

"Written by Joseph Fuardi de Fossau, Professor at Verceil during the vacations of 1786, who had been struck by the extreme ignorance of those persons who practised midwifery and the bad effects which often ensued from it.... He was ashamed that his pupils in surgery should not be better taught, and he constructed this figure for the purpose described in the above lines."

From this it is obvious that the female ivory manikins were used for instruction to teach students and midwives the anatomy of the body, and to demonstrate to them the position of the internal organs.

REVIEWS

Anatomie des Menschen. By HERMANN BRAUS. Bd. 2, 1924. (Julius Springer, Berlin.) Price 4.80 dollars.

The publication of the first volume of this text-book several years ago revealed a new spirit in German anatomy. Prof. Braus not only refused to limit the scope of his teaching to dead corpses but he made anatomy a live subject. He displayed a wider vision of the significance of structure and its relationship to function than perhaps any previous writer of a text-book.

His transference from Heidelberg to Würzburg in 1921 delayed the completion of the second volume until late in 1924.

It deals with the viscera of the thorax and abdomen, their gross and microscopic structure, and their functions in so far as they shed any light upon structure. The author does not hesitate to use any information, comparative, embryological, morphological, physiological or clinical that will help to make the significance of structure comprehensible. Therein lies its exceptional interest, which is further enhanced by its remarkable freedom from the tyranny of convention, the bugbear of most text-books of anatomy. But the feature of the book that first arrests attention is the excellence of the illustrations. Fig. 104—a free reconstruction of the essential anatomy of the lung by A. Vierling—is one of the most brilliant and illuminating drawings ever made to illustrate bodily structure; and there are scores of almost equally meritorious drawings in this remarkable book.

The death of the inspired author before the completion of the third (and concluding) volume is a real catastrophe. For Hermann Braus was a great master of anatomy, with rare breadth of vision and lucidity in exposition. Had he lived to complete his work it would unquestionably have been the greatest elementary text-book of anatomy, such a work as is urgently needed in our subject.

G. ELLIOT SMITH.

Handbuch der Biologischen Arbeitsmethoden. (Abderhalden.) Abt. 5, Teil 5 A, Heft 2. Methoden der Muskel- und Nervenphysiologie. Lief. 143. G.M. 5.40.

There are two monographs in this part of this work. The first (of 102 pages) is entitled "Theoretische Grundlagen der Gelenkmechanik" and is written by Grummel of Stuttgart. As is to be expected in the Abderhalden series, it covers concisely and well the matter of which it treats, in this instance the ordinary Dynamical Theory; but in the isolated and unapplied form in which it has reached us, it is difficult to express the usefulness that such a monograph may have or to indicate to whom it may be expected to appeal. The author, it is true, has drawn a few of his illustrations from the body, but throughout it is a mathematical treatise and an anatomist who had not already a sound knowledge of mathematics would not be able to understand so condensed a treatment as it presents; and while we believe that it is not so intended, it can hardly be written for the student of Dynamics. At the end of the article, for example, the writer gets the equations of motion of one and two jointed

systems, but these equations could readily be written by those with a rudimentary knowledge of Rigid Mechanics; it is not at all clear, however, to an anatomist what can be done with them when they are written. The references are almost entirely to the Teubner series of mathematical text-books and the only works with which an anatomist might be expected to be acquainted are those of O. Fischer, though there is no reference to his text-book *Theoretische Grundlagen für eine Mechanik der lebenden Körper* (Teubner, 1906). It will be understood, of course, that though we have not been able to discover in what way this article might assist the anatomist to understand the organic joint mechanisms, it is certainly an excellent summary of that which it treats.

The second article (of 54 pages) by E. Hirt of Münich is entitled "Graphische Methoden zur Darstellung normaler und pathologischer willkürlicher Bewegungsabläufe." The article opens with a short statement of the factors which must be considered in the analysis of a voluntary movement and proceeds to an account of how movements may be graphically represented; but the statement is short and, only two gross movements being selected, the account is somewhat limited. The larger part of the article deals with the comparison of the records of the movements of abnormal and normal states, Kraepelin's "writing apparatus" being used throughout; and here obviously the writer treats of matter in which he is highly specialised. Again, however, we feel, though a number of extremely interesting data are given, especially for example of delayed reaction times in abnormal muscular states, that the appeal the article will make is not to the anatomist, or even to the physiologist, but entirely to those who are working, as the author is, in a psychiatric field or perhaps to those engaged in the study of industrial fatigue, though fatigue as a factor of abnormal movement is not directly considered.

"Über die Körperproportionen der japanischen Feten." (Body proportions of the Japanese foetus.) By T. Akiba. *Folia Anatomica Japonica.* October, 1924. Vol. II, pp. 189–220.

The author investigates the question of the embryological racial differences between the European and Japanese foetus, which have been studied by Professor Kudo. This paper deals mainly with the question of the growth in length. He comes to the conclusion that the cause of the difference in height between the European and Japanese adult lies in the relative shortness of the lower extremities of the latter. On careful measurements of 160 Japanese and 164 European foetuses, the author investigates at what time, whether in uterus or after birth, this retardation in growth commences. He finds that there is no difference in the length of the lower extremities in the Japanese and European foetus. This equality persists until the seventh year after birth, when there is a standstill in the growth of the lower extremities of the Japanese child; this fact the author attributes to the peculiar sitting attitude which children have to assume, in accordance with the habits in Japan, in the years from 7 to 10. The author does not completely deny a certain racial difference, as a relative shortness of the tibia and fibula appears already in foetal life.

"Über den Atlas und Epistropheus bei den eingeborenen Formosanern." (The atlas and epistropheus of the natives of Formosa, Seiban.) By T. Tsusaki. *Folia Anatomica Japonica.* October, 1924. Vol. II, pp. 221–46.

Measurements of 22 atlantes and 20 epistrophei after the method of Kasebe, and a statement of the various differences in these bones. These dimensions are compared with those of other races.

"Über die Vergleichung einiger Fixierungs- und Färbungsmethoden." (A comparison between several staining and fixation methods.) By K. Kosaka and F. Bito. *Folia Anatomica Japonica.* October, 1924. Vol. II, pp. 247–52.

The methods compared were: fixation fluids—absolute alcohol, 80 per cent. alcohol, 10 per cent. formalin; each of these with 5 per cent. acetic acid; and the solutions of Carnoy, Müller, Zenker and Orth. The stains used were acids.

To show zymogen bodies in the pancreas it is best to fix with formalin, or Orth's solution. Alveolar and glandular cells are best fixed with alcohol and acetic acid. The acid dyes stain better after addition of some acid. In weak eosin stains alum solution may be used with advantage. With acid dyes it is possible to determine the degree of acidity in different tissues.

Radium, X-rays and the Living Cell: with Physical Introduction. By Hector A. Colwell, M.B. (Lond.), D.P.H. (Oxford), Assistant Radiologist, King's College Hospital, and Sidney Russ, D.Sc. (Lond.), F.Inst.P., Joel Professor of Physics, Middlesex Hospital Medical School. Revised and enlarged edition. 1924. London: G. Bell and Sons, Ltd. 21*s.* net.

In the second edition of this text-book the authors have described and collated the main experimental facts which have been established as to the effects of X-rays and radium upon living tissues.

The first edition, which appeared in 1915, was one of the earliest products of co-operation with a common aim between a medical man and a pure scientist.

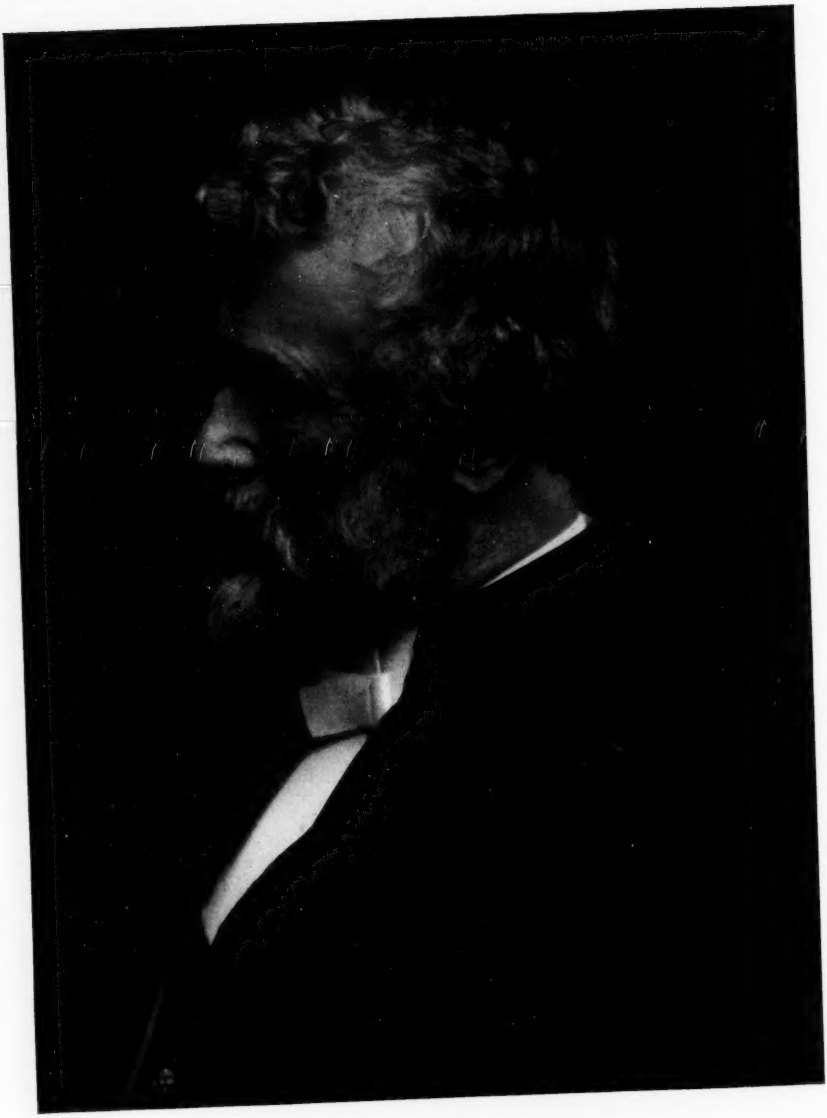
Part I opens with a physical section in which the fundamental facts are set forth in a lucid and comprehensive manner. Medical men and students need have no fear of getting out of their depth while reading this section.

Part II is devoted to an explanation of the action of X-rays and radium in varying dosages upon Seeds, Plants, Bacteria, Developing forms of Life, Skin, Blood-vessels, Blood, Spleen, Thymus and Thyroid, Alimentary tract, Nervous System, Eye and Connective Tissues.

The action of radium and X-rays upon malignant cells is fully discussed, and the nature and pathology of mouse sarcoma is clearly set forth and well illustrated by excellent microphotographs. The question of the production of Malignant Disease by X-rays and radium is discussed and experimental data given. A chapter on idiosyncrasy and dosage will be found useful.

After each chapter a complete bibliography is appended and these will be of the utmost value to those interested in any special branch of the subject.

This text-book is indispensable to all embryologists and surgeons who are interested in the uses of radiation from the experimental and therapeutic standpoint.



PROFESSOR CLELAND

OBITUARY NOTICE

The late Emeritus Professor JOHN CLELAND

John Cleland, M.D. (Edinburgh), LL.D. (St Andrews, Edinburgh and Glasgow), D.Sc. (Queen's University, Ireland), F.R.S., Emeritus Professor of Anatomy in the University of Glasgow, died at Lidsing, Kent, on 5th March, 1925, in his ninetieth year.

For many years Cleland had been the Nestor of British Anatomy, as, in his prime, he had been its Hercules both in intellect and in physique. Happily, his great leonine head—which would have delighted the eye of Michael Angelo—his imposing figure and the animation of his kindly spirit have been excellently preserved for posterity in two striking portraits painted by the late Sir George Reid, R.S.A., and presented, by his old students and friends on his retirement in 1909, one to the University of Glasgow and one to his family.

Through his father, a surgeon of high repute in the Royal Burgh of Perth, he came of Covenanter stock, and, in loyalty to the memory of an ancestor of his who fought at Drumclog on the side of the Covenant, he gave the name of that battlefield to his new home in Somerset. It may have been to this heritage that he owed the qualities which carried him with distinction through many a "bonnie fecht" on the fields of scientific controversy and academic polity. Certain it is that no one ever "preached and fenced" more zealously the ideals of high tradition and enlightened progress associated with the tenure of a Scotch University Chair.

A pupil of the Royal High School of Edinburgh, he completed his undergraduate studies at the University of that city while he was yet too young, by a year, to qualify for a medical degree; most of that year he spent by continuing his studies in France and Germany, interest in the problems of morphological science having been deeply stirred in his mind by the genius of his teacher, Prof. John Goodsir. In later years, in a paper ("On the relations of the Vomer, Ethmoid, and Inter-maxillary bones," *Phil. Trans.* 1863) considered by himself to be the most important of his own contributions to the solution of these problems, he gratefully acknowledged his debt to the influence of that great anatomist.

On his return to Edinburgh, to graduate in 1856, he was appointed by Goodsir as his Junior Demonstrator. The late Sir William Turner was Senior Demonstrator at the time. Surely the three composed a group unique and epoch-making in the annals of British Anatomy.

A few years later he went to assist Prof. Allen Thomson as Senior Demonstrator of Anatomy in the University of Glasgow, and in 1863 was appointed

to the Chair of Anatomy and Physiology in Queen's College, Galway, to which office were attached the duties of Surgeon to the Hospital. Mr T. P. O'Connor, M.P., the Father of the present House of Commons, who was at that time a student at Galway, has written of the strong impression made on the Irish mind by Cleland's striking personality, high ideals and sagacious Scotch humour. Cleland, on his side, often affectionately recalled the constant kindliness and loyalty he had received from his Irish students and colleagues; some impress of their long and close association would often peep out unconsciously in his conversation or be used whimsically to give the perfect turn of phrase or accent to some story from his perennial store of fun and wit.

It might well have been expected that the multifarious duties of his Chair in Galway would leave little time for the continuance of the investigations which had already made his name. Actually, however, the fourteen years he spent there proved the most fruitful in his career as regards the output of research. During this period he published a large number of erudite and highly-technical monographs, ranging widely over the scattered fields of Morphology, Physiology, Pathology, Histology, Anthropology, Embryology and Teratology—papers not only rich in observation and speculation but showing also a skill of delicate manipulation which is all the more striking in view of the fact that he had not resource to the many mechanical aids at the command of the investigator of to-day. The two text-books which he wrote then might serve still for models of elementary instruction; his *Animal Physiology* was for long unrivalled as the standard manual on the subject, and, though now superseded by much more elaborate treatises, has never been excelled; his *Directory for Dissection* is a wonderful example of concise yet fluent description and practical instruction. It was in Galway, too, that he edited, jointly with Sharpey and Allen Thomson, the 7th edition of Quain's *Anatomy*, his contributions to which were notable for many valuable additions to the accurate description of human anatomy. When it is remembered that in addition to these activities he had to carry on the constant and absorbing duties of a Hospital Surgeon, his energy and powers of concentration are cause for wonder. Yet this clinical work proved to be an invaluable asset, for from it he frequently culled wise little homilies on medical practice for the benefit of his students in later life, and, furthermore, it no doubt accounted for the remarkably *living* character which he imparted to all his teaching; as has been truly said of him—"One always felt when listening to him that he was speaking of the living and not of the dead."

When Allen Thomson retired in 1887, Cleland succeeded his old "Chief" as Regius Professor of Anatomy in the University of Glasgow. From then onward, to the end of his working days, Glasgow became his *Alma Mater* and none of her many distinguished sons ever served her more loyally than he. His accession added lustre to a Senate already rich in men of world-wide fame, worthy apostles of the ancient motto of their University—*VIA, VERITAS, VITA*. Kelvin, John and Edward Caird, Nichol, Jebb, Veitch and Gairdner were at

that time, like himself, at the zenith of their powers, forming a memorable constellation in the academic sky.

His new home in the Professors' Quadrangle became associated with the most sacred ties of his family life; there, intimate friends witnessed with deep admiration his tender devotion to the closing years of his aged mother's life; later, to this home he brought his bride, Miss Ada Balfour, eldest daughter of the late John Hutton Balfour, Professor of Botany in the University of Edinburgh, who was his rare helpmeet until her death in 1918 and one whose name will live for ever in the hearts of all who were privileged to share her friendship; and in this home their son, now the Rev. John R. Cleland, M.A., was born.

For thirty-two years thereafter he ministered to succeeding generations of students, winning ever-increasing respect and affection from them all; for, while his fame as a master grew, there was never any waning in the friendly interest and over-weening kindliness which he bestowed so freely on all who came in close personal contact with him; but, for the time, woe betided the hapless youth—or senior colleague even—who had the misfortune to provoke him to anger; his wrath was like the thunder of Boanerges, but, the lesson once driven home and repentance evoked, it very soon dissolved into a winsome benignity which will always be remembered affectionately by those who, in their student days, had learned both to fear and to love him.

During his earlier years in Glasgow, continued devotion to research produced from him a succession of important additions to scientific literature which are to be found in various scientific periodicals and, together with papers by his Demonstrators Principal J. Yule Mackay and Dr R. Bruce Young, in a volume entitled *Memoirs and Memoranda of Anatomy*.

When, in later years, he became the zealous and outstanding opponent of the great wave of materialistic interpetrations of Nature which followed closely on the epoch-making work of Charles Darwin, he became more and more involved in strenuous and sometimes bitter controversy, with the result that his energies became centred rather on the promulgation of his views as to the right interpretation of accepted facts.

The doctrine of evolution had always a strong appeal for him, and he was second to none in admiration of Darwin's contributions towards the solution of its problems; but he had no toleration for any but idealistic views of the operation of its laws. From profound study of natural phenomena he massed impressive arguments in favour of these views; of many papers which he wrote in support of them "The element of symbolic correlation in Expression," "Vision," "Terminal forms of life" and "The Classification of the Vertebrata" may be cited as containing the most effective expositions of his thesis that evolution is a "determinate process," not "blind," that matter affords no explanation of spirit but that "in the hidden ocean of infinite spirit lies locked the secret of matter."

The fertility of phrase, the facility of exposition and the high powers of

imagination evidenced in his scientific papers found freer scope in a volume of poems he published in 1887. *Scala Naturae*, the long poem which gives its name to the collection, abounds in striking lines. The keynote of this remarkable poem—

> Ah! Fantasy begone! and thou, serene,
> Majestic more than Fancy's noblest flight,
> Eternal Truth; clear browed like morn arises,
> Throw back the clouds of error rolling in
> And deign to guide an earnest wanderer.

—leads to a wide and general survey of his conception of the aspects of Nature which he had more particularly studied. Among the shorter poems, which testify to the catholicity of his Muse, is one *On the Loss of the "Eurydice,"* 1878, which illustrates well his close personal sympathy for his fellow men.

Closely allied to his poetic temperament were artistic gifts of a high order; these were shown not only in a keen interest in and wide knowledge of the work of the great Masters of painting and sculpture but also in the products of his own pencil and brush; they were very manifest too in the beauty of the preparation and presentation of the specimens comprising the remarkable Museum of Human and Comparative Anatomy he bequeathed to the University of Glasgow, which had been to him a life-long labour of love.

The *Text-Book of Human Anatomy*, which he wrote in later years in collaboration with Principal J. Yule Mackay, was likewise a labour of love. Into this book he gathered the rich fruits of a long experience of research and teaching. No better tribute could be paid to its merit than to quote from a review written for the *Edinburgh Medical Journal* by the late Prof. D. J. Cunningham, whose own notable success in the compilation of text-books was already firmly established:

> "One cannot read this book without being forced to think and without acquiring a feeling of reverence and admiration for the Anatomist who is able to speak authoritatively and from personal observation on so many varied and intricate morphological problems."

As a teacher he was somewhat lacking, to the mind of the average student, in the talent for presenting his subject in a systematic way. This was not due to any lack of patience or sympathy, for it was his constant aim to give his students all the practical help he could towards overcoming the difficulties of a crowded curriculum. It was due, rather, to the very richness of his store of learning and culture. Often, in the course of a lecture, some apparently trivial fact—some minute facet on a dry bone, for instance—would send him soaring to heights of disquisition whither it was quite beyond the capacity of any member of the class to follow. Nevertheless no one—not even the permanent occupant of the "back benches" where the "slackers" are wont to congregate —could fail to respond to the enthusiasm of his delivery or to be fascinated by the robust spirit of a great intellect which often scintillated with delightful outbursts of ever-fresh and even boisterous humour. Over and above the instruction which he laboured so unsparingly to give to them, his students,

and, indeed, all who were associated with him in any way, gained in full measure that indefinable inspiration towards vision and courage in the battle of life which is inseparable from the influence and memories of a really great teacher.

ALEX. MACPHAIL.

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